

Utah State University

DigitalCommons@USU

All Graduate Theses and Dissertations

Graduate Studies

5-2013

Legacy Effects of Habitat Degradation by Lesser Snow Geese on Ground-Nesting Savannah Sparrows along the Hudson Bay Lowlands

Stephen L. Peterson
Utah State University

Follow this and additional works at: <https://digitalcommons.usu.edu/etd>



Part of the [Other Life Sciences Commons](#)

Recommended Citation

Peterson, Stephen L., "Legacy Effects of Habitat Degradation by Lesser Snow Geese on Ground-Nesting Savannah Sparrows along the Hudson Bay Lowlands" (2013). *All Graduate Theses and Dissertations*. 1455.

<https://digitalcommons.usu.edu/etd/1455>

This Thesis is brought to you for free and open access by the Graduate Studies at DigitalCommons@USU. It has been accepted for inclusion in All Graduate Theses and Dissertations by an authorized administrator of DigitalCommons@USU. For more information, please contact digitalcommons@usu.edu.



LEGACY EFFECTS OF HABITAT DEGRADATION BY LESSER SNOW GEESE
ON GROUND-NESTING SAVANNAH SPARROWS ALONG
THE HUDSON BAY LOWLANDS

by

Stephen L. Peterson

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Wildlife Biology

Approved:

David N. Koons, PhD
Major Professor

Frank Howe, PhD
Committee Member

Kimberly A. Sullivan, PhD
Committee Member

Mark McClellan, PhD
Vice President for Research and Dean of
the School of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2013

Copyright © Stephen L. Peterson 2013

ALL RIGHTS RESERVED

ABSTRACT

Legacy Effects of Habitat Degradation by Lesser Snow Geese on
Ground-Nesting Savannah Sparrows along the Hudson Bay Lowlands

by

Stephen L. Peterson, Master of Science

Utah State University, 2013

Major Professor: Dr. David N. Koons
Department: Wildland Resources

Increased growth of the mid-continent population of Lesser Snow Geese (LSGO) has led to the degradation of coastal salt marsh and sedge meadow habitats across Canadian Arctic and sub-Arctic ecosystems. It is believed that a human-induced trophic cascade caused by agricultural habitat modification along migratory routes and wintering grounds has contributed to the increase in LSGO numbers, which has resulted in the alteration of habitat quality and connectivity along northern breeding and stopover sites used by various avian species. This habitat degradation has been shown to decrease the presence and temporal persistence of ground-nesting passerine and shorebird species at a local level and may lead to decreases of Arctic / sub-Arctic breeding avian species across landscapes that LSGO utilize and degrade.

In 1999, four paired study plots were established, and used in conjunction with a single study plot from 1976, in order to measure the composition of habitat parameters (barren ground extent; graminoid and shrub cover) and to estimate the number of avian

nests found in these plots. Using this historical data along with our findings from 2010 and 2011, our main objectives were to: 1) document the change in the aforementioned habitat parameters over time; 2) estimate the local nesting occupancy rates of the common Savannah Sparrow (SAVS), a robust and adaptable ground nester; and 3) determine which habitat variables are indicative of the rates of change and occurrence of nesting by SAVS within the study plots.

By using ANOVA, linear mixed effects, and multi-state occupancy models, results suggest that an increase in barren ground, decreases in shrub and graminoid cover, and a loss of connectivity between suitable nesting patches has led to a 10% ($\lambda = 0.90$) annual decline in the probability that SAVS nesting occurred across the study plots from 1999 to 2010.

These model results may be used to estimate long-term trends in persistence of breeding SAVS and other similar ground-nesting avian species that share habitats with LSGO along Arctic and sub-Arctic ecosystems.

PUBLIC ABSTRACT

Legacy Effects of Habitat Degradation by Lesser Snow Geese on
Ground-Nesting Savannah Sparrows along the Hudson Bay Lowlands

by

Stephen L. Peterson

Little is known of the direct and indirect legacy of Lesser Snow Goose (LSGO) habitat degradation in northern Canada on the biodiversity of other avian species. It is believed that a human-induced trophic cascade caused in part by agricultural habitat modification along migratory routes and wintering grounds has contributed to the increase in LSGO numbers, which has resulted in increased foraging pressure by LSGO on northern breeding and stopover sites. This habitat degradation may lead to decreased abundance and richness of Arctic / sub-Arctic avian species across landscapes that LSGO utilize and degrade.

Here we evaluated the annual change in vegetative cover (graminoids and shrubs) and how that may have influenced the nesting occurrence of the Savannah Sparrow (SAVS), a robust, adaptable ground nester, that relies on intact ground and shrub cover for nesting. Over a 10-year period (1999 to 2010) there was a 10% annual decline in the probability of SAVS nesting occurrence, driven by a loss of over half of the shrub cover, due to increased barren ground, over the same time period.

This research will provide information for managers about the broad risks of increasing numbers of LSGO and provide insight into ways to mitigate habitat degradation and trophic impacts on other species. It will also provide critical evaluation

of the impacts of habitat degradation by LSGO (a native invasive species) on natural resources, ecosystem services, and threatened and endangered species.

ACKNOWLEDGMENTS

First and foremost I would like to express my sincere thanks and appreciation to my loving partner and best friend, Carolee Lavery. Without her unyielding support, love, and encouragement, none of this would have been possible.

I cannot express enough sincere gratitude and appreciation I have for my advisor, David Koons, who was gracious enough to take me on as a graduate student and gave me the opportunity to work in one of the most beautiful and remarkable ecosystems on the earth. I feel extremely lucky to have had such an accomplished and knowledgeable ecologist / teacher to mentor and guide me through this scientific research process. His expertise, patience, friendship, and genuine caring is unparalleled.

A huge round of applause for my lab mate, David Iles, for his friendship, his mad rummy 500 and guitar playing skills, and his willingness to slug through the mud and muck, and the mosquito-infested skies with me, searching for the ever elusive Savannah Sparrow nest.

I would like to thank Robert “Rocky” Rockwell for sharing his incredible depth of knowledge and expertise about the Hudson Bay lowland ecosystems and its inhabitants. I am deeply appreciative of his friendship, overwhelming generosity, and the ample supply of bacon, steaks, and Jack Daniels in camp.

My vegetation and habitat work could not have been completed without the assistance and expertise of Chris Witte. A master naturalist of the area, his knowledge of the birds and plants was critical to my complete understanding of my study site.

I am grateful to those that provided friendship, guidance, and assistance throughout this research experience including lab mates Jeff Warren and Beth Ross, and my committee members, Frank Howe and Kim Sullivan, who were not only incredibly helpful with their scientific insight and the editing process of this thesis, but have also been very important mentors to me throughout my academic experience at Utah State University. A special acknowledgment goes out to my friend, Lise Aubry, who without complaining, followed behind me and recorded all my vegetation survey data.

I would like to acknowledge all those individuals that assisted in collecting both vegetation and bird nesting data throughout the years of this study.

A big thank you goes out to Jon Talon, our pilot, with Hudson Bay Helicopters in Churchill, MB. I truly appreciated his friendship, hospitality and generosity. Thank you to everyone at camp that assisted with nest searching, comfort station burnings, cooking, building, and your friendship including Frank and Kit Uvino, John Park, and Helen French. Special thanks to the DaSilva family at Gypsy's Bakery in Churchill, MB, who always made me feel welcomed and provided excellent meals and fond memories.

Financial support for this project was provided by USU's Quinney College of Natural Resources, the Seely-Hinckley Graduate Scholarship, The Hudson Bay Project, The American Museum of Natural History, and the Frank M. Chapman Memorial Fund. Wapusk National Park provided study and firearms permits for conducting work in the park.

Stephen L. Peterson

CONTENTS

	Page
ABSTRACT	iii
PUBLIC ABSTRACT	v
ACKNOWLEDGMENTS	vii
LIST OF TABLES	x
LIST OF FIGURES	xi
CHAPTER	
1. INTRODUCTION	1
2. LONG-TERM MODIFICATION OF SALT-MARSH HABITAT BY LESSER SNOW GEESE AT LA PÉROUSE BAY	13
3. IMPACTS OF LESSER SNOW GOOSE FORAGING ON THE OCCURRENCE OF SAVANNAH SPARROW NESTING.....	49
4. CONCLUSIONS	76

LIST OF TABLES

Table	Page
2.1. Linear mixed model results for annual changes in proportional cover of habitat classes on the Weatherhead study plot.....	35
2.2. Linear mixed model results for annual changes in habitat class patch size and distance between shrub patches on the Weatherhead study plot	36
2.3. Linear mixed model results for annual changes in proportional cover of habitat classes on all study plots	37
2.4. Linear mixed model results for annual changes in habitat class patch size and distance between shrub patches on all study plots.....	38
3.1. Parameter estimates for the top single season, multi-state occupancy model for Savannah Sparrow (<i>Passerculus sandwichensis</i>)	72
3.2. Top 10 single season, multi-state occupancy models for Savannah Sparrow (<i>Passerculus sandwichensis</i>)	73

LIST OF FIGURES

Figure	Page
2.1. Area map of study site	39
2.2. Generalized illustration of study plots	40
2.3. Proportional estimates of habitat classes on the Weatherhead study plot	41
2.4. Estimates of patch size of habitat classes and distance between shrub patches for the Weatherhead study plot	42
2.5. Proportional estimates of habitat classes on all study plots	43
2.6. Estimates of patch size of habitat classes and distance between shrub patches for all study plots	44
2.7. Historic and future estimated change in habitat class patch sizes on the Weatherhead study plot.....	45
2.8. Historic and future estimated change in habitat class patch sizes on all study plots	46
2.9. Historic and future estimated change in distance between shrub patches and shrub cover patch size on the Weatherhead study plot.....	47
2.10. Historic and future estimated change in distance between shrub patches and shrub cover patch size on all study plots	48
3.1. Estimated probabilities of ψ^2 for Savannah Sparrow (<i>Passerculus sandwichensis</i>) in relation to distance between shrub patch habitat	74
3.2. Derived estimates of ψ^{1*2} for Savannah Sparrow (<i>Passerculus sandwichensis</i>) in surveyed grid cells	75
3.3. 13 year period of number of days > 0° C in May and June in the Churchill, Manitoba, Canada area.....	76

CHAPTER 1

INTRODUCTION

Human-induced trophic cascades have had direct and indirect effects on biodiversity and ecosystems at both regional and local scales (Lindberg et al. 1998, Pace et al. 1999, Österblom et al. 2007). Anthropogenic mechanisms that have contributed to multi-species population declines and the degradation of their habitats include over-exploitation of species, direct and indirect introduction of non-native species, habitat modification, as well as the mismanagement of landscapes and resources (Folke et al. 1996, Pereira et al. 2012).

There are many examples of inverse population effects within a food-web, where increased pressure by a top-level consumer upon a basal producer can modify the rate of occurrence or the productivity of both the producer and mid-level consumer populations within a food chain, which is defined as a cascading event across trophic levels (Hairston et al. 1960, Strong 1992, Pace et al. 1999, Fortin et al. 2005, Byrnes et al. 2006).

Globally, trophic cascades have been reported most commonly in aquatic environments, such as the decrease of seal species and Steller's sea lions (*Eumetopias jubatus*) in western Alaska which may have been indirectly caused by overfishing of the pinnipeds main diet of mackerel, pollock and cod species by humans (Merrick et al. 1997). Depleted pinniped numbers may have in turn driven changes in killer whale (*Orcinus orca*) foraging behavior, such as switching from a focus of preying upon seals and sea lions (their preferred diet) to sea otters (*Enhydra lutris*) in the region (Estes et al. 1998). Consequently, this switch has led to a recent reduction in sea otter abundance,

which had rebounded from their historically reduced numbers due to overhunting by humans. This trophic cascade from fish to pinnipeds to whales and sea otter has even affected sea urchins and kelp forests further down the food chain. Sea otters are vital for controlling the number of urchins in this region, which if left unchecked, can decimate kelp forests. With the initial rebound in otter populations, urchin numbers were kept in check, which restored large coastal areas of kelp that were once barren and degraded (Estes and Duggins 1995).

Trophic cascades are not as well understood in terrestrial ecosystems. Polis et al. (2000) stated that trophic cascades in terrestrial ecosystems might be elusive because of the scattered and weak interactions between species. Croll et al. (2005) nevertheless provide evidence of a rare terrestrial trophic cascade created by human introduction of arctic foxes (*Alopex lagopus*) to certain islands of the Aleutian archipelago for the purpose of fur production. Predation by arctic foxes severely reduced populations of nesting seabirds, which transport oceanic nutrients to land in the form of guano, which contains phosphorus and nitrogen that contributes to high soil fertility. This then allows grasses to flourish, but in the absence of this nutrient-rich guano, these areas could not support productive grasslands and were transformed into a brush and forb dominated landscape.

These are just a few examples that illustrate how anthropogenic activities can create trophic cascades that dramatically alter ecosystem functioning, and consequently impact multiple species across local and regional areas. Over the past 40 years the mid-continent population of Lesser Snow Geese (*Chen caerulescens caerulescens*; LSGO) has grown by 5-14% per year (Alisauskas et al. 2011), which has been attributed to habitat

modifications of wintering grounds and migratory routes (Boyd et al. 1982). In these regions, increased agricultural production of rice and cereal-grain crops has led to drastic changes in the landscape as well as the energy available to migrating and wintering LSGO (Jefferies et al. 2004, Jefferies et al. 2006). Commensurate with these changes, the implementation of 1.5 million hectares of U.S. National Wildlife Refuges across the Mississippi and eastern Central flyways may have offered LSGO extra protection from hunting (Abraham et al. 2005*a*). Recently, there has been increased interest in converting set aside Conservation Reserve Program lands to the production of corn for expanding ethanol projects in the central and midwest U.S, which may exacerbate the problem of continuing growth of LSGO populations by providing them with even more food resources (Secchi et al. 2009, Wiens et al. 2011). In combination, these land modifications have led to and will continue to increase annual survival for LSGO (Rockwell et al. 1997, Cooch et al. 2001, Alisauskas et al. 2011, Abraham et al. 2012).

This expanding population of LSGO has consequently led to increased foraging pressure by the geese on salt-marsh graminoid roots and rhizomes during spring migration and on their northern breeding grounds, which has resulted in heavily degraded salt marsh habitats along the western Hudson Bay lowlands (Jano et al. 1998, Jefferies and Rockwell 2002, Jefferies et al. 2006). Overgrazing and root grubbing by LSGO has consequently altered soil salinity and entire plant assemblages, creating marginal habitat for the nesting colony of LSGO at La Pérouse Bay, Manitoba (Srivastava and Jefferies 1995, Abraham et al. 2005*b*, Jefferies et al. 2006). With the deterioration of LSGO nesting habitat quality since the mid-1970s, breeding numbers have declined at La

Pérouse Bay, and LSGO have moved to healthier vegetated sites in the larger Cape Churchill region (Cooch et al. 2001, Abraham et al. 2005a).

As populations expand and areas are degraded, LSGO have become considered by many as native invasive species (Valéry et al. 2009) that are having negative impacts on human-vested interests such as the aforementioned agricultural fields in the United States, where fall-seeded crops may be destroyed by overabundant LSGO that use these fields as stopover and wintering sites (Abraham et al. 2005a). Although there has been a localized decline in LSGO population growth at La Pérouse Bay, this has not yet reduced their overall population numbers at a regional scale. This growth has, however, caused a human-induced trophic cascade of negative impacts on various species and ecosystem processes associated with degraded supratidal marsh in the Arctic and sub-Arctic (Rockwell et al. 2003, Abraham et al. 2005a).

Examination of the degraded habitat sites at La Pérouse Bay has revealed not only alterations in the plant community and loss of species, but also a loss of important invertebrate species that many passerine species depend upon (Abraham et al. 2005a). In particular, spider and ground beetle species have been lost in these degraded areas as well as the loss of species richness amongst midge communities, which may affect nesting passerines, shorebirds, and waterfowl in the area (Milakovic et al. 2001, Milakovic and Jefferies 2003).

Indeed, breeding numbers of waterfowl, passerine and shorebirds have declined at La Pérouse Bay commensurate with the LSGO degradation of habitat (Rockwell et al. 2009). For example, Northern Shoveler (*Anas clypeata*) were once common in the supratidal habitats of La Pérouse Bay, where they foraged for zooplankton in ponds

throughout the historical LSGO colony area. But since the 1980s their local abundance has declined, possibly due to changes in water quality associated with LSGO habitat degradation (Rockwell et al. 2009). Semipalmated Sandpiper (*Calidris pusilla*) were once prolific breeders in the La Pérouse Bay area, with 133 nests found in 1983, declining to only six detected nests in 1999 (Rockwell et al. 2009). This may be attributed to a LSGO induced loss of graminoid vegetative cover, which the sandpiper depends upon for nesting cover.

Avian species of special concern may also be vulnerable to continuing habitat degradation by LSGO. For example, the Short-eared Owl (*Asio flammeus*) is a common ground-nesting species, which frequents sedge meadows and barrens within eastern portions of Wapusk National Park (Rockwell et al. 2009), and is a listed species of special concern (schedule 3) under the Canadian Government's Species at Risk Registry (<http://www.sararegistry.gc.ca>). Continuing degradation of quality nesting habitats by LSGO could have additional detrimental effects on this vulnerable species. Another species of special concern is the Yellow Rail (*Coturnicops noveboracensis*), which has been impacted by LSGO habitat degradation because of the rails' reliance on intact saltwater marshes dominated by sedges, grasses, and rushes. Detection of this secretive marsh bird has been rare since the mid-1980s (Rockwell et al. 2009), although in 2010 we did hear multiple individuals calling near our research camp in more intact habitats west of the heavily degraded LSGO colony.

Surprisingly, even the robust and adaptable Savannah Sparrow (*Passerculus sandwichensis*; SAVS) has declined in areas where LSGO have degraded the habitat. Dependent upon dwarf shrub cover (i.e. *Salix spp.*) for nesting, where shrubs replace tall

grasses in their more northern range (Wheelwright and Rising 2008), SAVS experienced a 77% decline in average nesting densities from the mid-1970s to 1999 (Weatherhead 1979, Rockwell et al. 2003). This was associated with a loss of > 50% of the shrub cover across a 7 ha study area (Rockwell et al. 2003).

However, the evidence for the deleterious trophic impacts of LSGO on other avian species is not concrete. Sammler et al. (2008) proposed that their data from a 3-year (1984, 1999, and 2000) project at a study site 15 km southeast of La Pérouse Bay showed an increase in abundance of tundra-nesting passerines and shorebirds across a 48 km² landscape. At a smaller spatial scale, when looking at heavily degraded sites, there was a reduction in species abundance. The impact of LSGO on other species may thus depend on spatial scale and the severity of degradation. The Cape Churchill study area used by Sammler et al. (2008) area is southward down the Hudson Bay coast from La Pérouse Bay and has only recently been invaded by large numbers of foraging LSGO. These areas have not yet reached the same point of degradation as observed around La Pérouse Bay (Jano et al. 1998). One must also take into account the annual environmental variability that occurs in the Canadian Arctic and sub-Arctic (Rockwell et al. 2009), which makes it all the more important to temporally and spatially replicate observations of avian population dynamics in the face of habitat degradation by LSGO.

Here we build upon historical vegetation surveys and SAVS nesting data from La Pérouse Bay to assess changes in habitat parameters over time and commensurate changes in nesting occupancy rates of SAVS, which given their adaptable nature, is an ideal indicator of the loss of quality nesting habitats due to severe habitat degradation by LSGO.

In Chapter 2 we use linear mixed models to quantify changes in vegetation ground cover (i.e. barren ground, graminoid cover, and shrub cover) across a 23 ha study site represented by both heavily degraded and marginally intact plots that can be found throughout the greater La Pérouse Bay area of supratidal marshes. In Chapter 3 we use a multi-state occupancy model to examine changes in rates of SAVS nesting occupancy. We incorporate findings from Chapter 2 in order to determine which habitat variables best explain changes in the annual variation of SAVS nesting occurrence. In Chapter 4 we conclude by discussing the negative ramifications that habitat degradation by LSGO may have on Arctic and sub-Arctic species assemblages and their ecosystems at both a local and regional scale; and how our research may provide knowledge in helping to address options for managing LSGO as a native invasive species. We finally discuss future directions in research that may be followed in continuing our investigation into the response of associated plants and animals in the Cape Churchill region to increasing numbers of LSGO.

References

- Abraham, K. F., R. L. Jefferies, and R. T. Alisauskas. 2005*a*. The dynamics of landscape change and Snow Geese in mid-continent North America. *Global Change Biology* 11:841-855.
- Abraham, K. F., R. L. Jefferies, and R. F. Rockwell. 2005*b*. Goose-induced changes in vegetation and land cover between 1976 and 1997 in an Arctic coastal marsh. *Arctic, Antarctic, and Alpine Research* 37:269-275.

- Abraham, K. F., R. L. Jefferies, R. T. Alisauskas, and R. F. Rockwell. 2012. Northern wetland ecosystems and their response to high densities of Lesser Snow Geese and Ross's Geese. Pages 9-45 *in* Evaluation of special management measures for midcontinent Lesser Snow Geese and Ross's Geese (J. O. Leafloor, T. J. Moser, and B. D. J. Batt, Eds.). Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service, Washington, D.C. and Canadian Wildlife Service, Ottawa, Ontario.
- Alisauskas, R. T., R. F. Rockwell, K. W. Dufour, E. G. Cooch, G. Zimmerman, K. L. Drake, J. O. Leafloor, T. J. Moser, and E. T. Reed. 2011. Harvest, survival, and abundance of midcontinent Lesser Snow Geese relative to population reduction efforts. *Wildlife Monographs* 179:1-42.
- Boyd, H., G. J. Smith, and F. G. Cooch. 1982. The Lesser Snow Goose of the eastern Canadian Arctic: Their status during 1964-1979 and their management from 1982 to 1990. *Canadian Wildlife Service Occasional Paper* 46:1-21.
- Byrnes, J., J. J. Stachowicz, K. M. Hultgren, A. R. Hughes, S. V. Olyarnik, and C. S. Thornber. 2006. Predator diversity strengthens trophic cascades in kelp forests by modifying herbivore behaviour. *Ecology Letters* 9:61-71.
- Cooch, E. G., R. F. Rockwell, and S. Brault. 2001. Retrospective analysis of demographic responses to environmental change: A Lesser Snow Goose example. *Ecological Monographs* 71:377-400.
- Croll, D. A., J. L. Maron, J. A. Estes, E. M. Danner, and G. V. Byrd. 2005. Introduced predators transform subarctic islands from grassland to tundra. *Science* 307:1959-1961.

- Estes, J. A., and D. O. Duggins. 1995. Sea otters and kelp forests in Alaska: Generality and variation in a community ecological paradigm. *Ecological Monographs* 65:75–100.
- Estes, J. A., M. T. Tinker, T. M. Williams, and D. F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282:473–476.
- Folke, C., C. S. Holling, and C. Perrings. 1996. Biological diversity, ecosystems, and the human scale. *Ecological Applications* 6:1018-1024.
- Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: Behavior shapes a trophic cascade in Yellowstone National Park. *Ecology* 86:1320-1330.
- Hairston, N., F. Smith, and L. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* 94:421-425.
- Jano, A. P., R. L. Jefferies, and R. F. Rockwell. 1998. The detection of vegetational change by multitemporal analysis of LANDSAT data: The effects of goose foraging. *Journal of Ecology* 86:93-99.
- Jefferies, R. L., and R. F. Rockwell. 2002. Foraging geese, vegetation loss and soil degradation in an Arctic salt marsh. *Applied Vegetation Science* 5:7-16.
- Jefferies, R. L., R. F. Rockwell, and K. F. Abraham. 2004. The embarrassment of riches: agricultural food subsidies, high goose numbers, and loss of Arctic wetlands a continuing saga. *Environmental Reviews* 11:193–232.
- Jefferies, R. L., A. P. Jano, and K. F. Abraham. 2006. A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology* 94:234-242.

- Lindberg, D. R., J. A. Estes, and K. I. Warheit. 1998. Human influences on trophic cascades along rocky shores. *Ecological Applications* 8:880-890.
- Merrick, R. L., M. K. Chumbley, and G. V. Byrd. 1997. Diet diversity of Steller sea lions (*Eumetopias jubatus*) and their population decline in Alaska: A potential relationship. *Canadian Journal of Fisheries and Aquatic Sciences* 54:1342–1348.
- Milakovic B., T. J. Carleton, and R. L. Jefferies. 2001. Changes in midge (Diptera: Chironomidae) populations of sub-arctic supratidal vernal ponds in response to goose foraging. *Ecoscience* 8:58–67.
- Milakovic B., and R. L. Jefferies. 2003. The effects of goose herbivory and loss of vegetation on ground beetle and spider assemblages in an Arctic supratidal marsh. *Ecoscience* 10:57–65.
- Österblom, H., S. Hansson, U. Larsson, O. Hjerne, F. Wulff, R. Elmgren, and C. Folke. 2007. Human-induced trophic cascades and ecological regime shifts in the Baltic Sea. *Ecosystems* 10:877-889.
- Pace, M., J. Cole, S. Carpenter, and J. Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* 14:483-488.
- Pereira, H. M., L. M. Navarro, and I. S. Martins. 2012. Global biodiversity change: The bad, the good, and the unknown. *Annual Review of Environment and Resources* 37:25-50.
- Polis, G. A., A. L. Sears, G. R. Huxel, D. R. Strong, and J. Maron. 2000. When is a trophic cascade a trophic cascade? *Trends in Ecology and Evolution* 15:473–475.
- Rockwell, R. F., E. G. Cooch, and S. Brault. 1997. Dynamics of the mid-continent population of Lesser Snow Geese – projected impacts of reductions in survival

and fertility on population growth rates. Pages 73–100 *in* Arctic ecosystems in peril: Report of the Arctic goose habitat working group (B. D. J. Batt, Ed.). Arctic Goose Joint Venture, Canadian Wildlife Service, Ottawa, and U.S. Fish and Wildlife Service, Washington, DC.

Rockwell, R. F., C. R. Witte, R. L. Jefferies, and P. J. Weatherhead. 2003. Response of nesting Savannah Sparrows to 25 years of habitat change in a snow goose colony. *Ecoscience* 10:33-37.

Rockwell, R. F., K. F. Abraham, C. R. Witte, P. Matulonis, M. Usai, D. Larsen, F. Cooke, D. Pollak, and R. L. Jefferies. 2009. The Birds of Wapusk National Park. Wapusk National Park of Canada Occasional Paper #1. Winnipeg, Manitoba. Parks Canada.

Sammler, J. E., D. E. Andersen, and S. K. Skagen. 2008. Population trends of tundra-nesting birds at Cape Churchill, Manitoba, in relation to increasing goose populations. *Condor* 110:325-334.

Secchi, S., P. W. Gassman, J. R. Williams, and B. A. Babcock. 2009. Corn-based ethanol production and environmental quality: A case of Iowa and the conservation reserve program. *Environmental Management* 44:732-44.

Srivastava, D. S., and R. L. Jefferies. 1995. Mosaics of vegetation and soil salinity: A consequence of goose foraging in an arctic salt marsh. *Canadian Journal of Botany* 73:75-83.

Strong, D. R. 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. *Ecology* 73:747-754

- Valéry, L., H. Fritz, J. C. Lefeuvre, and D. Simberloff. 2009. Invasive species can also be native. *Trends in Ecology and Evolution* 24:585.
- Weatherhead, P. J. 1979. Ecological correlates of monogamy in tundra-breeding Savannah Sparrows. *Auk* 96:391-401.
- Wheelwright, N. T., and J. D. Rising. 2008. Savannah Sparrow (*Passerculus sandwichensis*). *In* The Birds of North America, no. 45 (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/045>.
- Wiens, J., J. Fargione, and J. Hill. 2011. Biofuels and biodiversity. *Ecological Applications* 21:1085-1095.

CHAPTER 2
LONG-TERM MODIFICATION OF SALT-MARSH HABITAT
BY LESSER SNOW GEESE AT LA PÉROUSE BAY

Summary

Intensive foraging by an increasing population of lesser snow geese (*Chen caerulescens caerulescens*; LSGO) has led to severe degradation of coastal lowland habitat in the Arctic and sub-Arctic. Here, we add to an impressive body of research conducted over the past 35 years along the western Hudson Bay lowlands by examining the legacy effects of LSGO herbivory and grubbing on vegetation assemblages in supratidal salt-marshes. In parallel with an avian study, we conducted research on a 23 ha study plot in the center of La Pérouse Bay, Manitoba that was historically home to a very large LSGO nesting colony. In 2010 we surveyed the study area for proportions of barren ground, graminoid and shrub cover, habitat patch size, and distance between shrub patches, and compared those changes over a 35-year period with historical vegetation data from 1976 and 1999. We found an overall increase in exposed, hyper-saline soils (barren ground) and significant declines in graminoid and shrub cover. Patches of barren ground increased by an average of 8% per year, leading to the eventual loss of > 50% of the shrub cover across the entire study area. Our findings agree with past experiments indicating that once snow geese push habitat degradation past a threshold, the system continues to move toward an alternative state with little to no chance of vegetation re-establishment. This habitat alteration has had, and will continue to have, significant deleterious impacts on the biodiversity of both plant and wildlife assemblages across

those areas that LSGO utilize and exploit. Continued evaluation of vegetation changes, recovery potential, and identification of areas that may be vulnerable to the expansion of LSGO is thus needed, and will allow managers to judge which Arctic and sub-Arctic ecosystems are vulnerable to degradation.

Introduction

Increased growth of the mid-continent population of LSGO has led to the degradation of coastal salt-marsh and sedge meadow habitats across Canadian Arctic and sub-Arctic ecosystems. In the past 40 years, LSGO have shown a 5-14% annual increase (Alisauskas et al., 2011), driven primarily by agricultural modifications and associated nutrient subsidies on their wintering grounds and migratory stopover areas (Boyd et al., 1982; Abraham et al., 2005*b*). Intensive overgrazing and grubbing of salt-marsh graminoid roots and rhizomes during spring migration and on their northern breeding grounds has consequently altered soil salinity and entire plant assemblages (Srivastava and Jefferies, 1995, 1996), creating marginal habitat not only for LSGO, but other ground-nesting avian species, which rely on intact and contiguous patches of graminoids and shrubs for nesting cover and foraging.

This habitat alteration is most evident at La Pérouse Bay, Manitoba; the site of a historically persistent colony of LSGO (Abraham et al., 2005*a*; Jefferies et al., 2006). With the deterioration of habitat quality since the mid-1970s, the breeding colony of LSGO have moved to healthier vegetated sites within the greater Cape Churchill region, leaving behind increased areas of barren ground with hyper-saline soils, which have had a

continuing negative impact on the remaining vegetation (Cooch et al., 2001; Abraham et al., 2005b).

Over the past 30 plus years, the late Dr. Robert L. Jefferies and colleagues conducted an impressive body of research on the interactions and consequences of LSGO grubbing on salt-marsh vegetation communities of the Arctic and sub-Arctic. Seminal work has included the description and comparison of the salt-marsh vegetation communities of La Pérouse Bay to other similar ecosystems (Jefferies et al., 1979); changes in the composition of vegetation species and assemblages through LSGO exclusion (Bazely and Jefferies, 1986); the possibility of habitat regeneration in the face of extensive grubbing and degradation by LSGO (Handa et al., 2002); and soil characteristics, along with other abiotic variables which have dramatically altered the salt-marsh habitat of La Pérouse Bay (Kerbes et al., 1990; Hik et al., 1992; Srivastava and Jefferies, 1995; Jefferies and Rockwell, 2002; Jefferies et al., 2006).

Using LANDSAT imagery, Jefferies et al. (2006) showed that between 1973 and 1999, over 35,000 ha of intertidal salt-marsh habitat had been lost across nine study sites within the Hudson Bay and James Bay region (along ~ 2,000 km of coastline), due to LSGO herbivory, which led to an alternative state of the ecosystem where recovery of vegetation is nearly irreversible in the exposed hyper-saline sediment. Within the immediate coastal habitats of La Pérouse Bay (along ~ 30 km of coastline), LANDSAT imagery showed a decline in vegetation cover of 2,454 ha between 1973 and 1993 (Jano et al., 1998).

Change in vegetation assemblages of La Pérouse Bay was examined from the ground between 1976 and 1997 (pre- and post LSGO colony growth) within five unique

regions (Abraham et al., 2005a). All five regions exhibited significant change, the extent of which depended on the region. The characteristics of the ground and shrub cover assemblages were dramatically altered due to LSGO disturbance, especially in the intertidal and supratidal salt-marsh areas, where losses of the *Puccinellia phryganodes*/*Carex subspathacea* (P-C) and the *Calamagrostis deschampsoides*/*Festuca rubra* (C-F) assemblages gave way to larger extents of barren ground. The frequency of the low willow and mixed shrub (i.e. *Salix* and *Betula spp.*) assemblages increased further inland of the supratidal marsh where fresh water and good drainage was available, but declined in poorly drained areas of the intertidal marsh.

Iacobelli and Jefferies (1991) investigated the loss of dwarf shrub willows (i.e. *Salix brachycarpa*) brought about by substantial increases in the salinity of expanding bare soils. They were able to show that within heavily grubbed areas by LSGO, soil temperatures were higher than intact areas due to the loss of an insulating layer of the late successional C-F assemblage. This primary ground cover is the first to be exposed in early spring after snowmelt. Found inland from tidal flats in the dwarf shrub (i.e. *Salix* and *Betula spp.*), LSGO seek out this graminoid assemblage to grub their roots and rhizomes. Loss of the C-F assemblage led to the formation of large expanses of peat barrens where higher soil temperatures led to increased evapotranspiration, which allowed salts to become concentrated in the soil water. This increased salinity led to premature leaf drop by dwarf shrubs, resulting in low survival and increased death of shrub communities.

Rockwell et al. (2003) assessed the change in vegetation cover from 1976 to 1999 at a finer scale, using a 7 ha study plot (subdivided into 50 m² grid cells) established by

Weatherhead (1979) within the supratidal salt-marsh habitat of La Pérouse Bay. Over that 23-year period, shrub assemblage (i.e. *Salix* and *Betula spp.*) declines ranged from 46% to 94% with barren ground increases of 51% to 423%, differing spatially between sample grid cells. In 1976 few shrubs were in poor condition, but by 1999, the increase in hyper-saline barren ground had significantly contributed to 89% of shrubs dying.

Here we re-examine the same 7 ha study plot, and include multiple paired sites of historically degraded and marginal habitats within the immediate area, using vegetation characteristic data from 1976, 1999, and 2010. The objective of this study was to assess the transition of vegetation states over 35 years (Handa et al., 2002; Bestelmeyer et al., 2009); specifically, whether vegetation conditions have improved or continued to deteriorate since the departure of the historically abundant LSGO colony that eventually sought out better quality habitats (although some geese still use the area). We first estimated proportional changes in 3 habitat classes (i.e. barren ground, graminoid cover, shrub cover), and then assessed change in patch size of each habitat class along with the distance between shrub cover patches, which provided insight into the extent of habitat fragmentation. Given the experimental findings of Jefferies and colleagues, we predicted an increase in barren ground because of the legacy over-grazing by LSGO has on soil dynamics, with concomitant declines in graminoid and shrub cover. We moreover predicted that such changes would result in more fragmented and discontinuous patches of quality shrub habitat for ground-nesting birds.

Methods

Study Area

Study plots were located on coastal supratidal salt-marsh habitat near La Pérouse Bay, approximately 30 km east of Churchill, Manitoba, Canada (58° 52.3' N, 93° 41.0' W), which is part of the western Hudson Bay Lowlands and within the northern boundary of Canada's Wapusk National Park (Fig. 2.1).

Vegetation of the study area is characterized by dwarf shrub species (i.e. *Salix*, *Betula spp.*), and the salt-marsh grass (e.g. *Puccinellia phryganodes*) and sedge species (e.g. *Carex subspathacea*) that LSGO prefer to forage on by grubbing and shoot pulling (Jefferies et al. 2004). With the increased foraging by LSGO on these graminoids, larger extents of hyper-saline soils are now more common throughout the general area. For more details on soil and vegetation interactions of the study area, see Iacobelli and Jefferies (1991), Srivastava and Jefferies (1995), and Jefferies and Rockwell (2002).

Vegetation Plots

Classification of vegetation and habitat condition was conducted on five study plots, which were set up in a grid system of 50 m² cells and included portions of a 1976 study site (7 ha) established to investigate the relationship between mating systems of Savannah sparrows (*Passerculus sandwichensis*; SAVS) and habitat quality (Weatherhead 1979). In addition to this long-term plot, four nearby study plots were established in 1999, representing heavily degraded habitats (2 plots, one of 3 ha and the other 5 ha) and marginally intact habitats (2 plots, one of 3 ha and the other 5 ha) that

were geographically adjacent and representative of the habitats surrounding La Pérouse Bay.

All plots were re-established in 2010 by finding original northwest corners of each plot with GPS coordinates and then using wooden stakes, rebar poles, and flagging to establish corners of each 50 m² grid cell. Each cell was identified by a unique study plot name (i.e. Weatherhead, Close-to-Camp, Japanese Gardens) and an alpha-numeric system for identifying each grid cell. Grid cell columns ran north to south and were labeled with letters; rows ran east to west and were labeled with numbers (Fig. 2.2).

Vegetation sampling was conducted on one plot in 1976, and on all five study plots in 1999 and 2010. Duplicating the same sampling procedure used by Weatherhead (1979) and Rockwell et al. (2003), 28 grid cells in 1976 and 92 grid cells in 1999 and 2010 were surveyed during the summer. A modified step-point method was used to classify the type of vegetation and habitat condition underfoot at each ~1 meter pace, along two diagonal transects within each cell (Evans and Love, 1957; Owensby, 1973; Rockwell et al., 2003; Abraham et al., 2005a). One observer walked each transect and called out a predetermined alpha-numeric code at each pace that identified vegetation species and/or habitat condition to a recorder that followed behind.

With the exception of 1976, all shrubs, grasses, sedges, and forbs were identified to genus and some to species level. Shrub height was recorded and condition was classified as either dead (100% dead branches), in poor condition (>1/3 dead branches), or healthy and alive (<1/3 dead branches). Habitat status in 1976 fell into one of six categories: barren ground, pond, sedge-short grass, mixed grass-short willow, *Elymus* (*Leymus arenarius*), and other *Salix spp.* (Weatherhead, 1979; Rockwell et al., 2003).

The objective of vegetation surveys in 1999 and 2010 was to assess whether habitat conditions had remained the same, improved or degraded further on all plots. Given the differential detail of vegetation recording over time, habitat status was reduced into three classes for analysis: barren ground, graminoid cover, and shrub cover; a level of detail suitable for defining habitat quality for ground-nesting avian species on the study plots that could be affected by LSGO habitat degradation. The barren ground class consisted of all bare soils, ephemeral ponds and streambeds, algal mats, mosses, and forbs (i.e. *Salicornia borealis*, *Senecio congestus*, *Atriplex glabriuscula*) indicative of disturbance and hyper-saline soils, and completely dead shrubs with no growth or ground cover. All grass and sedge species were included in the graminoid cover class, and the shrub cover class included all living or partially living shrubs (i.e. *Salix spp.*, *Betula glandulosa*, and *Myrica gale*) (Rockwell et al., 2003).

Data Analysis

The total number of paces from both diagonal transects within each grid cell were summed, and the proportion of each habitat class was then calculated. These proportional data were then transformed using the logit transform: $\log(y/[1-y])$, with the addition of a small value (+0.0001) to the denominator and numerator of the equation for graminoid and shrub cover proportion (due to some values close to or equal to zero), and subtraction of a small value (-0.0002) from the barren ground proportion (due to some values close to 1.0). This ensures that the transformed data does not include undefined values ($-\infty$ and ∞), and that proportional estimates fall between 0 and 1. Given the monotonic nature of

the logit transform, estimated coefficients are naturally interpreted within a linear model (as opposed to an arcsine transformation; Warton and Hui, 2011).

To determine if there were significant changes in proportion of the three habitat classes (barren ground, graminoid cover, and shrub cover) over time, and to determine the proper fixed effect (i.e. year) model structure for later analyses, an initial multivariate analysis of variance (MANOVA) was run in Program R (using the vector of proportional cover among the 3 habitat classes as the multivariate response). A comparison of habitat changes between 1976, 1999, and 2010 was conducted first on the Weatherhead study plot ($n = 28$), since the paired study plots had not been established prior to 1999. All plots were then analyzed together as one single study area ($n = 92$) between 1999 and 2010. Three separate model structures were compared to one another: a null model, a time trend model, and a model with year treated as a factor. To determine the best model structure for temporal change in habitat cover, we used Akaike's Information Criterion adjusted for sample size (AICc; Akaike, 1973), which Burnham and Anderson (2002, 2004) strongly recommend for its ability to assign a greater penalty for extra parameters.

Based on the best-performing MANOVA model structure for temporal change in habitat cover, a generalized linear mixed effects model (GLMM) was developed using the lme4 package in R (with a Gaussian distribution and identity link; Bates et al., 2011). In each GLMM, year was treated as a fixed effect and grid cell nested within study plot was treated as a random effect. This accounted for grid cell and study plot heterogeneity in the model structure but allowed us to focus our attention on temporal change in vegetation cover and habitat conditions, which was of primary interest (Bolker, 2008).

To adequately investigate avian ground-nesting habitat quality on all study plots, we also measured an index of mean patch size of all three habitat classes, estimated from the average number of sequential paces within a habitat class along both diagonal transects in a grid cell, and mean distance between shrub patches, estimated from the average summed number of both graminoid and barren ground paces between points where live shrubs were recorded. This parameter was essential in addressing the connectivity of quality nesting habitat patches, where the shrub component is critical for many ground-nesting birds. Analysis of habitat patch size and distance between shrub patches was similar to the analyses of habitat cover described above; however, we log-transformed the mean step length data to meet assumptions of normality (Kutner et al., 2004).

The Delta method (Seber, 1982; Cooch and White, 2006) was used to calculate the variance of each derived habitat parameter, where the squared derivative of the relationship between the derived and transformed parameters was multiplied by the square of each estimate's standard error (i.e., $(dy/dx)^2 * se^2$). Confidence intervals (95%) were then obtained.

To derive a rate of annual change for each habitat class, λ , we used the geometric growth equation: $\lambda = (N_{t+x} / N_t)^{(1/x)}$, where N is the proportional cover of a given habitat class at time t and x is the deviation in time between measurements (Gotelli, 2008).

Results

Weatherhead Study Plot (1976, 1999, 2010)

Proportional cover: The initial MANOVA analysis indicated that treating year as a factor was the best parameterization of temporal change in proportional cover of the three habitat classes (barren ground, shrub cover, and graminoid cover) on the Weatherhead study plot ($\Delta AIC_c = 23.69$ for year treated continuously and 294.68 for the null model). Proportional cover of each class differed significantly among the years of study (all $P < 0.001$).

After implementing these findings into a linear mixed model to account for random variation amongst the grid cells (i.e., a model with a fixed year effect treated as a factor and a random effect for grid cells), we found that the proportion of barren ground increased over the course of the study while the proportion of graminoid and shrub cover both decreased (Table 2.1 and Fig. 2.3). The annual rate of geometric increase in the proportion of barren ground was 1.04 between 1976 to 1999, which then slowed to a rate of 1.02 between 1999 and 2010. Concurrently, the proportional graminoid cover declined at a rate of 0.99 between 1976 and 1999, and although the absolute change was less, the rate of decline was even more severe ($\lambda = 0.98$) between 1999 and 2010. Similarly, the annual rate of loss in shrub cover between 1976 and 1999 was 0.95, and this rate of loss also accelerated between 1999 and 2010 ($\lambda = 0.94$).

Patch characteristics: The proportional increase of barren ground and the decrease in graminoid and shrub cover over the long-term study led to the fragmentation of contiguous patches of shrub cover. Initial MANOVA analysis of the mean patch size of each habitat class, and distance between patches of shrub cover yielded a top model

structure with year treated as a factor ($\Delta AIC_c = 128.54$ for year treated continuously and 440.07 for the null model). All four habitat parameters showed significant difference ($P < 0.001$) among the years of study.

These results were then used to develop a linear mixed model, such as the one described above for the analysis of habitat class proportions. The index to mean patch size of barren ground increased between 1976 and 1999 by approximately 1.5 m, but increased fourfold (~ 6.6 m) between 1999 and 2010. This led to an overall decrease in mean patch size of shrub cover by approximately 6.5 m from 1976 to 1999, with a smaller decrease of only 0.3 m from 1999 to 2010. This same trend was seen in the mean patch size of graminoids, which decreased by approximately 2.5 m between 1976 and 1999, with little to no change between 1999 and 2010. From 1976 to 1999 the distance between shrub patches decreased by approximately 1.3 m. However, from 1999 to 2010, there was an increase in the mean distance between shrub patches of approximately 5.1 m, coinciding with an increase in barren ground and a decrease in shrub cover proportions (Table 2.2 and Fig. 2.4).

All Study Plots (1999, 2010)

Proportional cover: All study plots were analyzed simultaneously for the years 1999 and 2010. Given the two points in time, initial MANOVA analysis of habitat class proportions gave equal weight to treating year as a trend or as a factor in the parameterization of the temporal change in proportional cover ($\Delta AIC_c = 71.87$ for the null model). All three habitat class proportions were found to differ significantly between the 11-yr period (barren ground and shrub cover $P < 0.001$; graminoid cover $P < 0.05$).

For consistency we estimated changes in proportional cover using a linear mixed model with year treated as a factor and parameterized a random effect for grid cells nested within study plots. The proportion of barren ground significantly increased between 1999 and 2010, associated with a sharp decrease in both the graminoid and shrub cover proportions over the same time period (Table 2.3 and Fig. 2.5). Barren ground proportions increased at the annual rate of 1.03. Proportions of graminoid and shrub cover declined at an annual rate of 0.96 and 0.91, respectively.

Patch characteristics: Initial MANOVA analysis of the habitat patch parameters also showed that year treated as a trend or as a factor received equal support ($\Delta\text{AIC}_c = 53.10$ for the null model) for estimating temporal changes in patch size and distance between shrub cover patches. There were significant differences between 1999 and 2010 for barren ground and shrub cover patch size, and distance between shrub patches ($P < 0.001$), but the difference in graminoid cover patch size between 1999 and 2010 was not significant ($P = 0.4203$), which coincided with little change in graminoid cover proportion over the same time interval (see above).

Using the same linear mixed model structure as that used for the proportional analysis, mean patch size of barren ground increased significantly by 7.5 m across the 11-yr period. In turn, this increased the average distance between patches of shrub habitat from 6.4 to 13.6 m, practically doubling the isolation distance. Both graminoid and shrub patch size decreased, albeit in smaller increments than the barren ground patch size (Table 2.4 and Fig. 2.6).

Discussion

Our study has effectively illustrated the consequence(s) of increased foraging and grubbing pressure by LSGO on the supratidal marsh habitat of La Pérouse Bay over 35 years. Building on the findings of Rockwell et al. (2003), we found an overall increase in barren ground habitat and significant declines in graminoid and shrub cover. A once healthy supratidal salt-marsh ecosystem has been degraded to the point that it has shifted into an alternative state that is of little value to most endemic wildlife (Rockwell et al., 2003; Milakovic et al., 2001; Milakovic and Jefferies, 2003), although some local avian species may benefit with increased barren areas which they prefer for nesting, including semipalmated plover (*Charadrius semipalmatus*) and horned lark (*Eremophila alpestris*) (Beason, 1995; Nol and Blanken, 1999).

We found that within the vegetative cover classes, the shrub assemblage declined most abruptly over time across the entire study area. On the Weatherhead study plot alone, over 41% of shrub cover was lost between 1976 and 2010, and more than half of all shrub cover was lost between 1999 to 2010 across all study plots (Figs. 2.3 and 2.5). Although graminoid cover declined on all plots over the study (Figs. 2.3 and 2.5), it did not decline as rapidly as the shrub cover. This is because many of the graminoids are more tolerant of hyper-saline conditions than the shrubs (Jefferies et al., 1979; Handa et al., 2002; Rockwell et al., 2003). Persistence of graminoid patches suggests that some re-vegetation may be possible in locations with suitable freshwater conditions, unconsolidated sediment and vegetative fragments (i.e. cover of residual graminoids and/or dead or dying shrubs), which can facilitate nitrogen fixing such that clonal propagation may take place (Handa and Jefferies, 2000; Rockwell pers. comm., 2011;

Abraham et al., 2012). The potential for “re-growth” of some plant assemblages has been observed within experimental exclosures on the study area, but not to the extent that would encourage re-establishment across the entire degraded area (Abraham et al., 2012).

The precipitous decline in vegetative cover occurred in parallel with significant increases in the proportion and patch size of barren ground across all study plots. Annual geometric increases in patch size of barren ground were significantly larger and grew at a faster pace after 1999, limiting shrub and graminoid cover. These findings corroborate the experiments conducted by Srivastava and Jefferies (1995) at a larger scale, who found that as patch size of barren ground increases, soil water salinity increases, subsequently limiting re-colonization by shrub and graminoid assemblages (Fig. 2.7 and 2.8).

Continued growth of barren ground patches will exacerbate this problem even when LSGO are completely absent from the area due to the salinity and erosion mechanisms explained above, creating a new alternative state of the ecosystem characterized by bare sediment, algal mats, mosses, and areas generally prone to invasion by forbs indicative of disturbance and hyper-saline soils (i.e. *Salicornia borealis*, *Senecio congestus*, *Atriplex glabriuscula*; Handa et al., 2002).

With increased patch size of barren ground, the connectivity of shrub cover was lost, which could negatively affect the breeding success of many ground-nesting birds in the study area, especially the SAVS that uses low-lying dwarf shrubs in place of tall grasses as nesting cover in the northern limit of its range (Wheelwright and Rising, 2008). Rockwell et al. (2003) showed a 77% decline in average nesting densities of SAVS on the Weatherhead study plot between 1976 and 1999, which was attributed to the extensive loss of shrubs during the same period.

Given observed changes in the state of shrub cover and distance between shrub patches, we predict that these habitat metrics will continue to change in the near future at the rates most recently observed (Figs. 2.7 and 2.8). Shrub patches may be reduced to less than 1 m in size with exponential increases in the distance between patches further fragmenting any viable habitat connectivity. Continued monitoring of these habitat changes at decadal intervals would nevertheless help determine threshold and stability properties of habitat change originally induced by LSGO foraging activities (Rumpff et al., 2011).

Our findings support the predictions and mechanistic explanations of how LSGO foraging leads to a degraded state of the ecosystem (Holling, 1973; Hik et al., 1992) characterized by extensive hyper-saline soils (Srivastava and Jefferies, 1996). A shift towards these conditions may be irreversible and inhibit the recovery of certain ground-cover assemblages, such as the dwarf shrubs that many ground-nesting birds depend upon in the Arctic and sub-Arctic (Iacobelli and Jefferies, 1991; van de Koppel et al., 1997; Jefferies and Rockwell, 2002). The expansion of localized degradation to a larger regional scale across the coast of western Hudson Bay is likely, and would have deleterious impacts on not only the plant community, but also invertebrate and vertebrate biodiversity (Jefferies et al., 2006). Given these potential threats to lowland ecosystems in the north, we agree with the recommendations set forth by Abraham et al. (2012): 1) ground evaluations of vegetation changes should be conducted along the entire western coast and southern portion of Hudson Bay; 2) assessment of the potential for vegetation assemblages to recover from LSGO degradation should continue; 3) areas of highest potential for expansion of breeding LSGO populations should be identified; and 4) efforts

should be invested in estimating the spatial carrying capacity for sustaining LSGO in North America, such that managers can judge the full extent to which Arctic and sub-Arctic ecosystems might be vulnerable to LSGO degradation.

References

- Abraham, K. F., Jefferies, R. L., and Rockwell, R. F., 2005a: Goose-induced changes in vegetation and land cover between 1976 and 1997 in an Arctic coastal marsh. *Arctic, Antarctic, and Alpine Research*, 37: 269–275.
- Abraham, K. F., Jefferies, R. L., and Alisauskas, R. T., 2005b: The dynamics of landscape change and snow geese in mid-continent North America. *Global Change Biology*, 11: 841–855.
- Abraham, K. F., Jefferies, R. L., Alisauskas, R. T., and Rockwell, R. F., 2012: Northern wetland ecosystems and their response to high densities of lesser snow geese and Ross's Geese. In: Leafloor, J. O., Moser, T. J., and Batt, B. D. J. (eds.), *Evaluation of Special Management Measures for Midcontinent Lesser Snow Geese and Ross's geese*. Arctic Goose Joint Venture, U.S. Fish and Wildlife Service, Washington, DC and Canadian Wildlife Service, Ottawa, Ontario, 9–45.
- Akaike, H., 1973: Information theory and an extension of the maximum likelihood principle. In: Petran B. N., and Csaki, F. (eds.), *2nd International Symposium on Information Theory*. Akademiai Kiado, Budapest, Hungary, 267–281.
- Alisauskas, R. T., Rockwell, R. F., Dufour, K. W., Cooch, E. G., Zimmerman, G., Drake, K. L., Leafloor, J. O., Moser, T. J., and Reed, E. T., 2011: Harvest,

- survival, and abundance of midcontinent lesser snow geese relative to population reduction efforts. *Wildlife Monographs*, 179: 1–42.
- Bates, D., Maechler, M., and Bolker, B., 2011: lme4: Linear mixed-effects models using S4 classes. R package version 0.999375-33. <<http://lme4.r-forge.r-project.org/>>, accessed 6 February, 2011.
- Bazely, D. R., and Jefferies, R. L., 1986: Changes in the composition and standing crop of salt-marsh communities in response to the removal of a grazer. *The Journal of Ecology*, 74: 693–706.
- Beason, R. C., 1995: Horned Lark (*Eremophila alpestris*). In: Poole, A. (ed.), *The Birds of North America Online*. Ithaca: Cornell Lab of Ornithology, <<http://bna.birds.cornell.edu/bna/species/195>>, retrieved 1 September, 2012.
- Bestelmeyer, B. A., Tugel, J., Peacock Jr., G. L., Robinett, D. G., Shaver, P. L., Brown, J. R., Herrick, J. E., Sanchez, H., and Havstad, K. M., 2009: State-and-transition models for heterogeneous landscapes: A strategy for development and application. *Rangeland Ecology and Management*, 62: 1–15.
- Bolker, B. M., 2008: *Ecological Models and Data in R*. Princeton, New Jersey: Princeton University Press, 408 pp.
- Boyd H., Smith, G. J., and Cooch, F. G., 1982: The lesser snow goose of the eastern Canadian Arctic: their status during 1964-1979 and their management from 1982 to 1990. *Canadian Wildlife Service Occasional Paper*, 46: 1–21.
- Burnham, K. P., and Anderson, D. R., 2002: *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Second Edition. New York: Springer-Verlag, 498 pp.

- Burnham, K. P., and Anderson, D. R., 2004: Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods and Research*, 33: 261–304.
- Cooch, E. G., Rockwell, R. F., and Brault, S., 2001: Retrospective analysis of demographic responses to environmental change: a lesser snow goose example. *Ecological Monographs*, 71: 377–400.
- Cooch, E. G., and White, G. C., 2006: *Program MARK: a gentle introduction*. Ninth Edition. <http://www.phidot.org/software/mark/docs/book/>, retrieved 1 September, 2009.
- Evans, R. T., and Love, R. M., 1957: The step-point method of sampling – a practical tool in range research. *Journal of Range Management*, 10: 208–212.
- Gotelli, N. J., 2008: *A Primer of Ecology*. Fourth Edition. Sunderland, MA: Sinauer Associates, Inc., 291 pp.
- Handa, I. T., and Jefferies, R. L., 2000: Assisted revegetation trials in degraded salt-marshes. *Journal of Applied Ecology*, 37: 944–958.
- Handa, I. T., Harmsen, R., and Jefferies, R. L., 2002: Patterns of vegetation change and the recovery potential of degraded areas in a coastal marsh system of the Hudson Bay lowlands. *Journal of Ecology*, 90: 86–99.
- Hik, D. R., Jefferies, R. L., and Sinclair, A. R. E., 1992: Foraging by geese, isostatic uplift and asymmetry in the development of salt-marsh plant communities. *Journal of Ecology*, 80: 395–406.
- Holling, C. S., 1973: Resilience and stability of ecological systems. *Annual Review of Ecology and Systematics*, 4: 1–23.
- Iacobelli, A., and Jefferies, R. L., 1991: Inverse salinity gradients in coastal marshes and

- the death of *Salix*; the effects of grubbing by geese. *Journal of Ecology*, 79: 61–73.
- Jano, A. P., Jefferies, R. L., and Rockwell, R. F., 1998: The detection of vegetational change by multitemporal analysis of LANDSAT data: the effects of goose foraging. *Journal of Ecology*, 86: 93–99.
- Jefferies, R. L., Jensen, A., and Abraham, K. F., 1979: Vegetational development and the effect of geese on vegetation at La Pérouse Bay, Manitoba. *Canadian Journal of Botany*, 57: 1439–1450.
- Jefferies, R. L., and Rockwell, R. F., 2002: Foraging geese, vegetation loss and soil degradation in an Arctic salt marsh. *Applied Vegetation Science*, 5: 7–16.
- Jefferies, R. L., Rockwell, R. F., and Abraham, K. F., 2004: The embarrassment of riches: agricultural food subsidies, high goose numbers and loss of Arctic wetlands – a continuing saga. *Environmental Review (Natural Resource Council Canada)*, 11: 193–232.
- Jefferies, R. L., Jano, A. P., and Abraham, K. F., 2006: A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology*, 94: 234–242.
- Kerbes, R. H., Kotanen, P. M., and Jefferies, R. L., 1990: Destruction of wetland habitats by lesser snow geese: a keystone species on the west coast of Hudson Bay. *Journal of Applied Ecology*, 27: 242–258.
- Kutner, M. H., Nachtsheim, C. J., Neter, J., and Li, W., 2004: *Applied Linear Statistical Models*. Fifth Edition. Chicago, IL: McGraw-Hill/Irwin, 1396 pp.
- Milakovic B., Carleton, T. J., and Jefferies, R. L., 2001: Changes in midge (Diptera:

- Chironomidae) populations of sub-arctic supratidal vernal ponds in response to goose foraging. *Ecoscience*, 8: 58–67.
- Milakovic B., and Jefferies, R. L., 2003: The effects of goose herbivory and loss of vegetation on ground beetle and spider assemblages in an Arctic supratidal marsh. *Ecoscience*, 10: 57–65.
- Nol, E., and Blanken, M. S., 1999: Semipalmated Plover (*Charadrius semipalmatus*), In: Poole, A. (ed.), *The Birds of North America Online*. Ithaca: Cornell Lab of Ornithology, <<http://bna.birds.cornell.edu/bna/species/444>>, retrieved 1 September, 2012.
- Owensby, C. E., 1973: Modified step-point system for botanical composition and basal cover estimates. *Journal of Range Management*, 26: 302–303.
- Rockwell, R. F., Witte, C. R., Jefferies, R. L., and Weatherhead, P. J., 2003: Response of nesting Savannah sparrows to 25 years of habitat change in a snow goose colony. *Ecoscience*, 10: 33–37.
- Rumpff, L., Duncan, D. H., Vesk, P. A., Keith, D. A., and Wintle, B. A., 2011: State-and-transition modelling for adaptive management of native woodlands. *Biological Conservation*, 144: 1224–1236.
- Seber, G. A. F., 1982: *The estimation of animal abundance and related parameters*. Second Edition. New York: Wiley, 672 pp.
- Srivastava, D. S., and Jefferies, R. L., 1995: Mosaics of vegetation and soil salinity: a consequence of goose foraging in an arctic salt marsh. *Canadian Journal of Botany*, 73: 75–83.

- Srivastava, D. S., and Jefferies, R. L., 1996: A positive feedback: herbivory, plant growth, salinity, and the desertification of an Arctic salt-marsh. *Journal of Ecology*, 84: 31–42.
- van de Koppel, J., Rietkerk, M., and Weissing, F. J., 1997: Catastrophic vegetation shifts and soil degradation in terrestrial grazing systems. *Trends in Ecology and Evolution*, 12: 352–356.
- Warton, D. I., and Hui, F. K. C., 2011: The arcsine is asinine: the analysis of proportions in ecology. *Ecology*, 92: 3–10.
- Weatherhead, P. J., 1979: Ecological correlates of monogamy in tundra-breeding Savannah sparrows. *Auk*, 96: 391–401.
- Wheelwright, N. T., and Rising, J. D., 2008: Savannah Sparrow (*Passerculus sandwichensis*), In: Poole, A. (ed.), *The Birds of North America Online*. Ithaca: Cornell Lab of Ornithology, <<http://bna.birds.cornell.edu/bna/species/045>>, retrieved 1 September, 2009.

TABLE 2.1. Linear mixed model results for changes in proportional cover of barren ground, graminoid, and shrubs on the Weatherhead study plot across 1976, 1999, and 2010 on the logit-transformed scale. In all cases, 1976 represents the intercept and coefficients for other years are estimated relative to the intercept. Proportional estimates and 95% confidence intervals are also shown. The grid-cell random effect shows the variance (Var) amongst the cells in the study plot on the logit scale (all rounded to the second decimal). The formula used in the lme4 package was: `habitat class ~ as.factor(year) + (1|cell_id)`.

Habitat Class	Year	β	S.E.	Prop.	95% C.I.	Random Effect Cell Var
Barren ground	1976	-1.10	0.10	0.25	(0.21 – 0.29)	0.09
	1999	1.71	0.11	0.65	(0.60 – 0.70)	
	2010	2.34	0.11	0.78	(0.74 – 0.82)	
Graminoid cover	1976	-1.15	0.11	0.24	(0.19 – 0.29)	0.10
	1999	-0.42	0.14	0.17	(0.15 – 0.20)	
	2010	-0.73	0.14	0.13	(0.11 – 0.16)	
Shrub cover	1976	-0.06	0.10	0.49	(0.48 – 0.49)	0.11
	1999	-1.56	0.12	0.17	(0.16 – 0.17)	
	2010	-2.37	0.12	0.08	(0.06 – 0.10)	

TABLE 2.2. Linear mixed model results for changes in habitat patch size of barren ground, graminoid, and shrub cover, and distance between shrub patches on the Weatherhead study plot across 1976, 1999, and 2010 on the log-transformed scale. In all cases, 1976 represents the intercept and coefficients for other years are estimated relative to the intercept. Habitat patch size estimates and 95% confidence intervals are also shown. The grid-cell random effect shows the variance (Var) amongst the cells in the study plot on the log scale (all rounded to the second decimal). The formula used in the lme4 package was: habitat patch size (or distance) ~ as.factor(year) + (1|cell_id).

Habitat Class	Year	β	S.E.	Size Est. (m)	95% C.I.	Random Effect Cell Var
Barren ground	1976	1.43	0.07	4.16	(3.56 – 4.77)	0.04
	1999	0.31	0.09	5.66	(5.35 – 5.97)	
	2010	1.08	0.09	12.32	(9.91 – 14.72)	
Graminoid patch	1976	1.51	0.05	4.52	(3.91 – 5.12)	0.01
	1999	-0.96	0.06	1.74	(1.55 – 1.93)	
	2010	-0.95	0.06	1.74	(1.55 – 1.93)	
Shrub patch	1976	2.09	0.04	8.06	(6.71 – 9.41)	0.00
	1999	-1.61	0.06	1.62	(1.32 – 1.91)	
	2010	-1.84	0.06	1.28	(1.01 – 1.55)	
Distance	1976	2.17	0.08	8.73	(5.89 – 11.57)	0.06
	1999	-0.17	0.09	7.35	(7.14 – 7.57)	
	2010	0.36	0.09	12.54	(11.78 – 13.31)	

TABLE 2.3. Linear mixed model results for changes in proportional cover of barren ground, graminoid, and shrubs across all study plots between 1999 and 2010 on the logit-transformed scale. In all cases, 1999 represents the intercept and the coefficient for 2010 is estimated relative to the intercept. The grid-cell random effect shows the estimated variance (Var) amongst grid cells in a given study plot on the logit scale (all rounded to the second decimal). The formula used in the lme4 package was: `habitat class ~ as.factor(year) + (plot|cell_id)`.

Habitat Class	Year	β	S.E.	Prop.	95% C.I.	Random Effect	
						Plot ID	Cell Var
Barren ground	1999	0.43	0.08	0.61	(0.59 – 0.62)	ccb	0.01
	2010	0.94	0.09	0.80	(0.77 – 0.82)	cgc	0.17
						jgb	0.91
						jgg	0.41
						wh	0.06
						Residual	0.34
Graminoid cover	1999	-1.45	0.09	0.19	(0.15 – 0.23)	ccb	0.00
	2010	-0.53	0.12	0.12	(0.11 – 0.13)	cgc	0.11
						jgb	10.86
						jgg	0.26
						wh	0.00
						Residual	0.63
Shrub cover	1999	-1.51	0.08	0.18	(0.15 – 0.22)	ccb	0.56
	2010	-1.11	0.11	0.07	(0.05 – 0.08)	cgc	0.56
						jgb	1.16
						jgg	0.70
						wh	0.56
						Residual	0.73

TABLE 2.4. Linear mixed model results for changes in habitat patch size of barren ground, graminoid, and shrub cover, and distance between shrub patches across all study plots between 1999 and 2010 on the log-transformed scale. In all cases, 1999 represents the intercept and the coefficient for 2010 is estimated relative to the intercept. The grid-cell random effect shows the estimated variance (Var) amongst grid cells in a given study plot on the log scale (all rounded to the second decimal). The formula used in the lme4 package was: habitat patch size (or distance) ~ as.factor(year) + (plot|cell id).

Habitat Class	Year	β	S.E.	Size Est. (m)	95% C.I.	Random Effect	
						Plot ID	Cell Var
Barren ground	1999	1.68	0.05	5.38	(4.51 – 6.24)	ccb	0.00
	2010	0.87	0.06	12.88	(11.55 – 14.21)	ccg	0.04
						jgb	0.12
						jgg	0.09
						wh	0.04
						Residual	0.17
Graminoid cover	1999	0.65	0.10	1.92	(1.67 – 2.16)	ccb	0.00
	2010	-0.23	0.14	1.53	(1.44 – 1.62)	ccg	0.00
						jgb	13.15
						jgg	0.00
						wh	0.00
						Residual	0.84
Shrub cover	1999	0.57	0.06	1.77	(1.66 – 1.89)	ccb	1.70
	2010	-0.37	0.08	1.22	(1.15 – 1.30)	ccg	1.70
						jgb	1.70
						jgg	1.70
						wh	1.70
						Residual	0.30
Distance Between	1999	1.92	0.05	6.84	(5.54 – 8.15)	ccb	0.01
	2010	0.68	0.06	13.57	(12.45 – 14.68)	ccg	0.02
						jgb	0.14
						jgg	0.12
						wh	0.04
						Residual	0.17

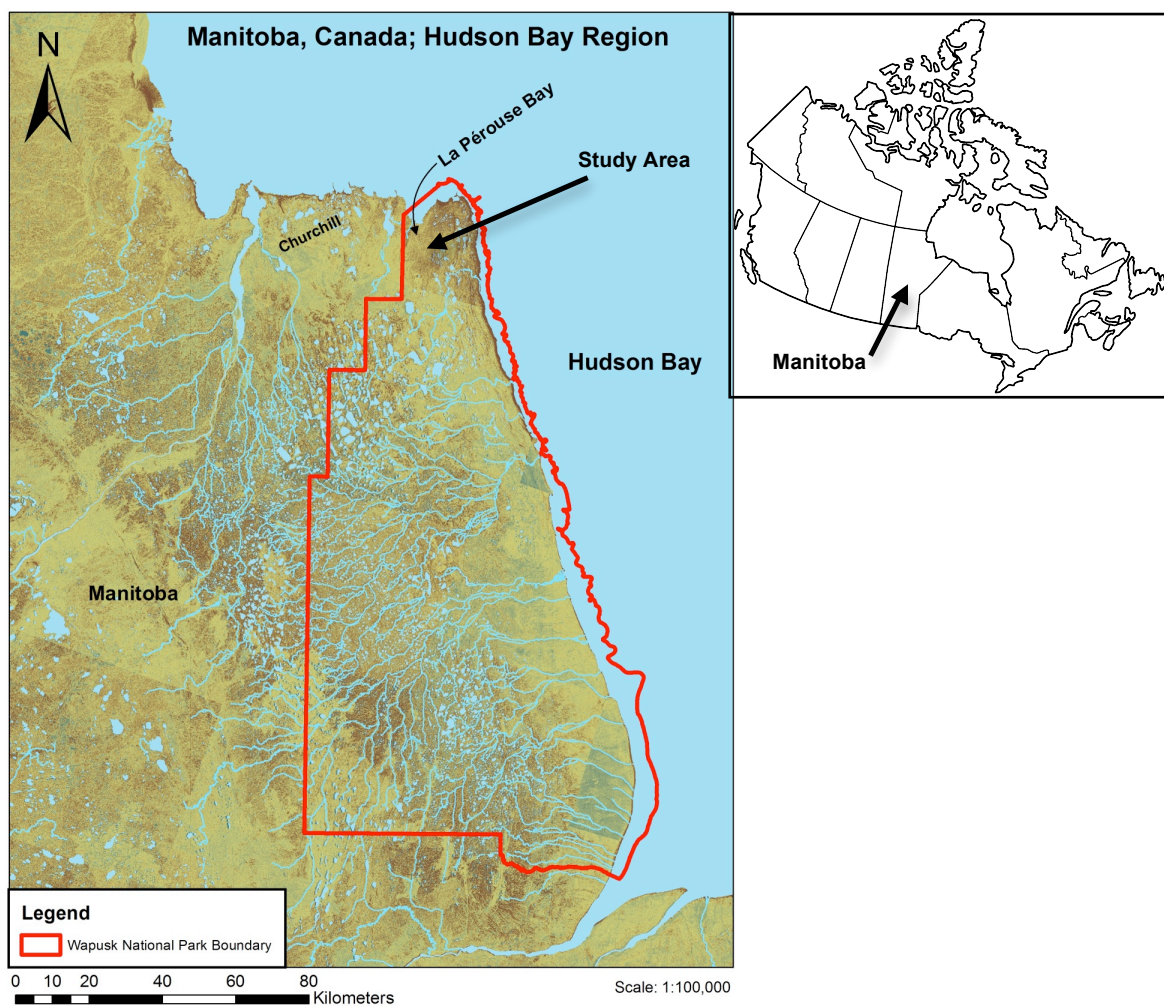


FIGURE 2.1. Area map of study site location approximately 30 km east of Churchill, Manitoba, Canada. General study area is identified by bold black arrow.

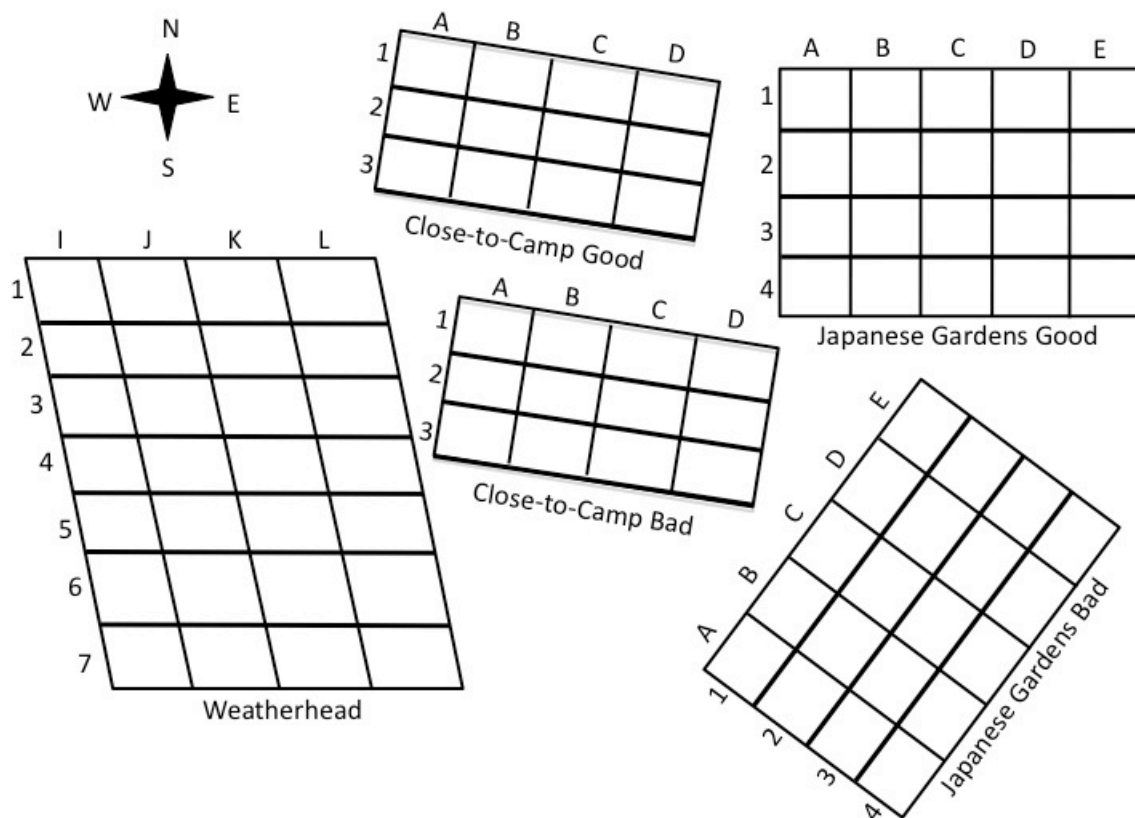


FIGURE 2.2. Generalized illustration of study plots, associated names and approximate location to each other. Each grid cell is 50 m².

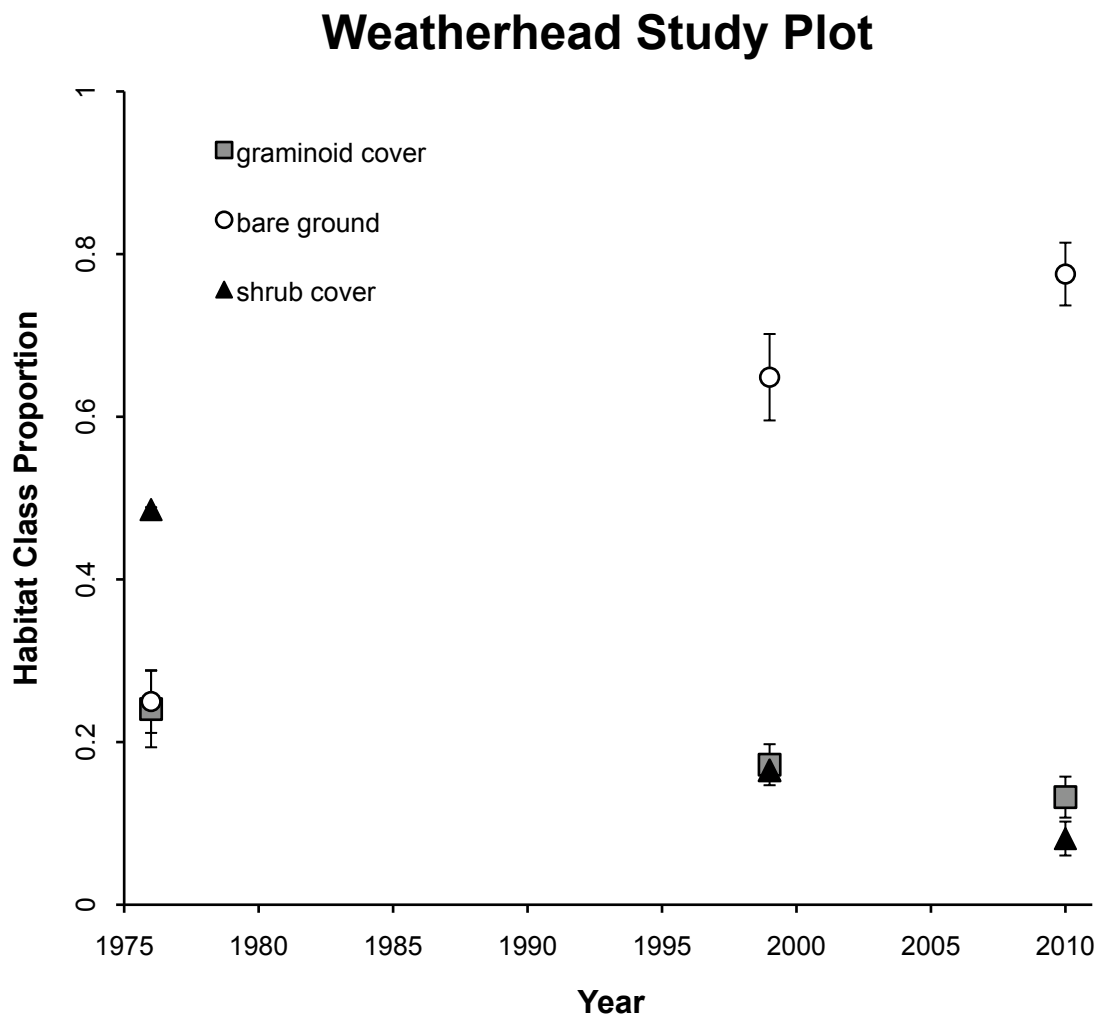


FIGURE 2.3. Proportional estimates with 95% confidence intervals of habitat classes (i.e. barren ground, graminoid cover, and shrub cover) on the Weatherhead study plot for 1976, 1999, and 2010.

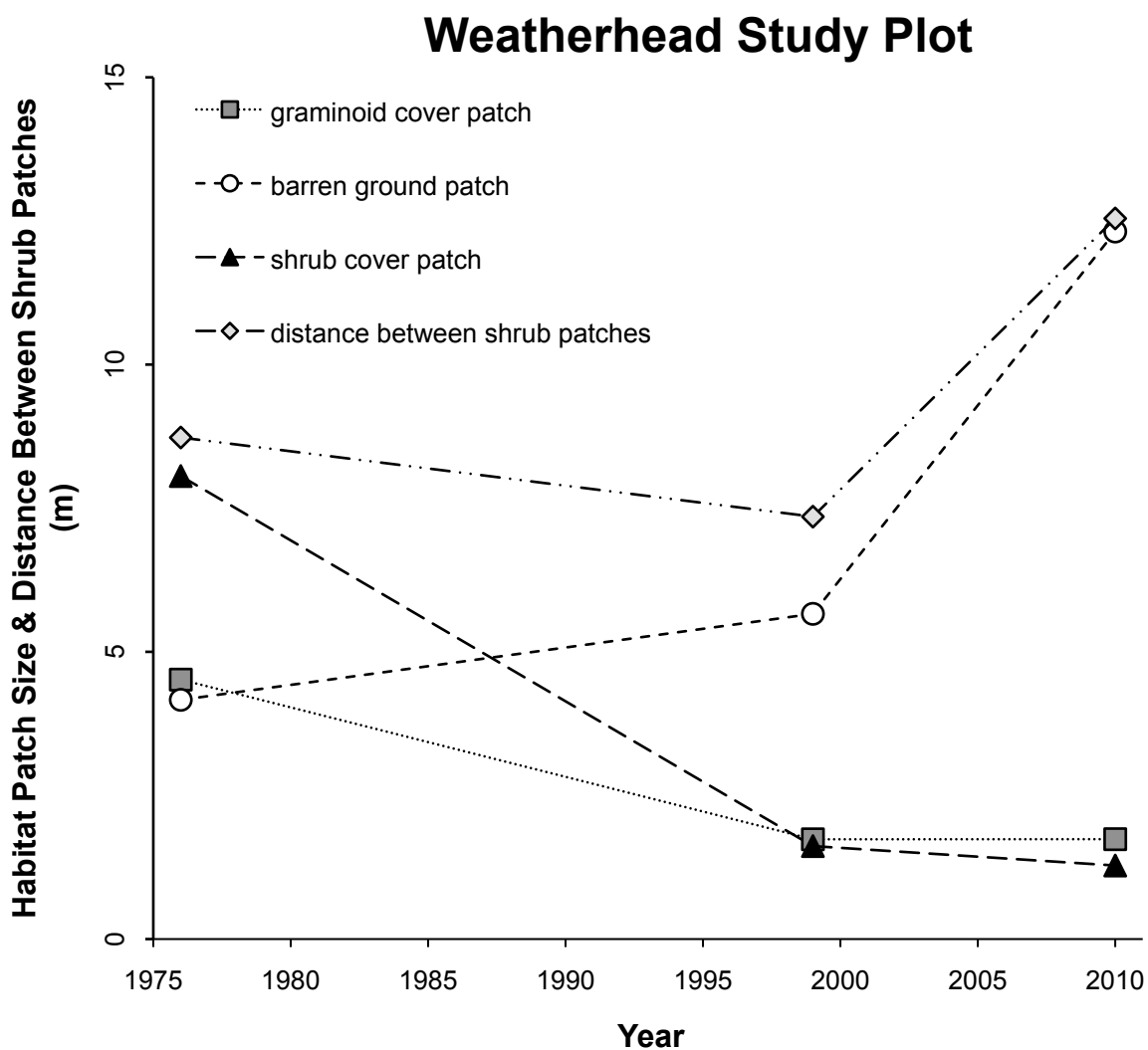


FIGURE 2.4. Patch size (m) estimates with trend line (95% confidence intervals not shown because of their small size relative to the symbol size; see Table 2.2 for precision) of habitat classes (i.e. barren ground, graminoid cover, and shrub cover) for the Weatherhead study plot, and estimates of distance between shrub patches for 1976, 1999, and 2010

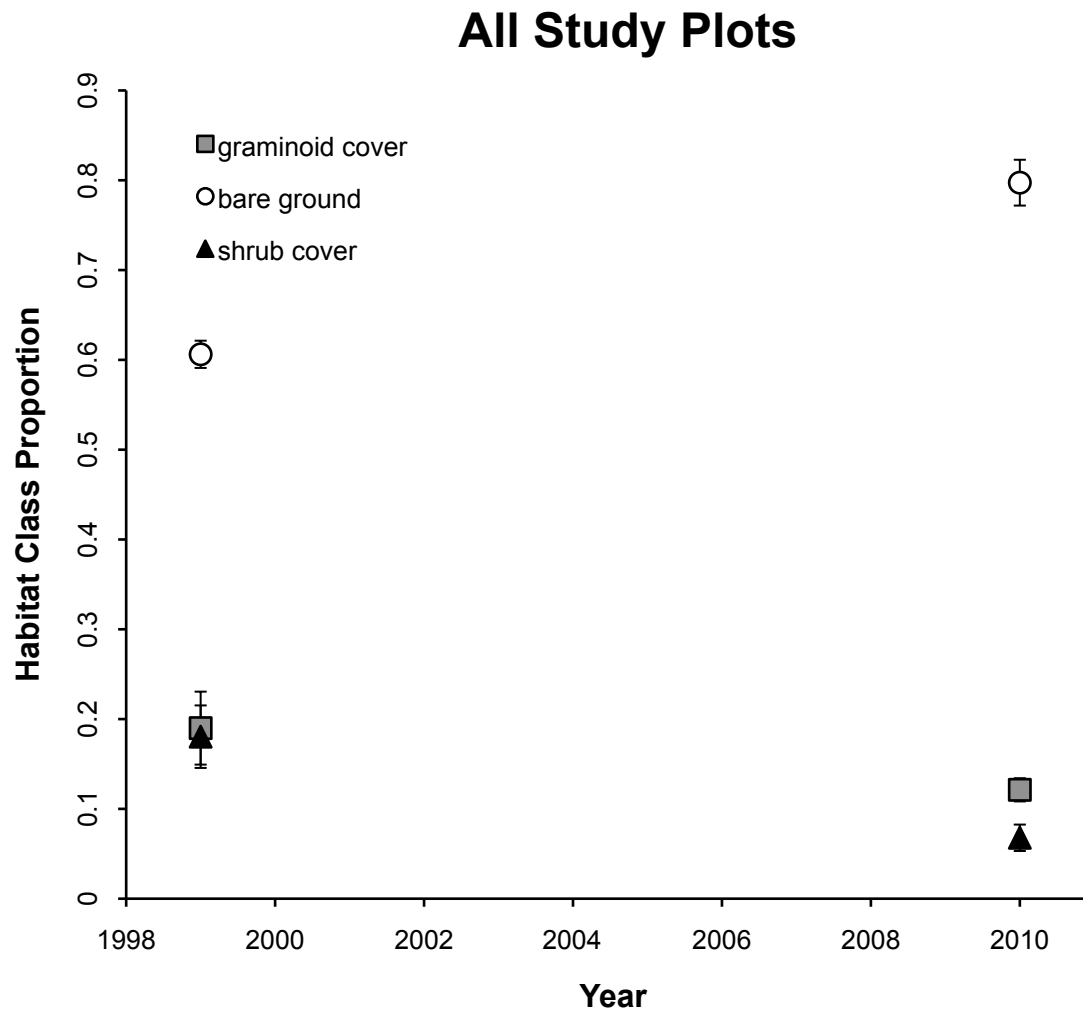


FIGURE 2.5. Proportional estimates with 95% confidence intervals of habitat classes (i.e. barren ground, graminoid cover, and shrub cover) on all study plots for 1999 and 2010.

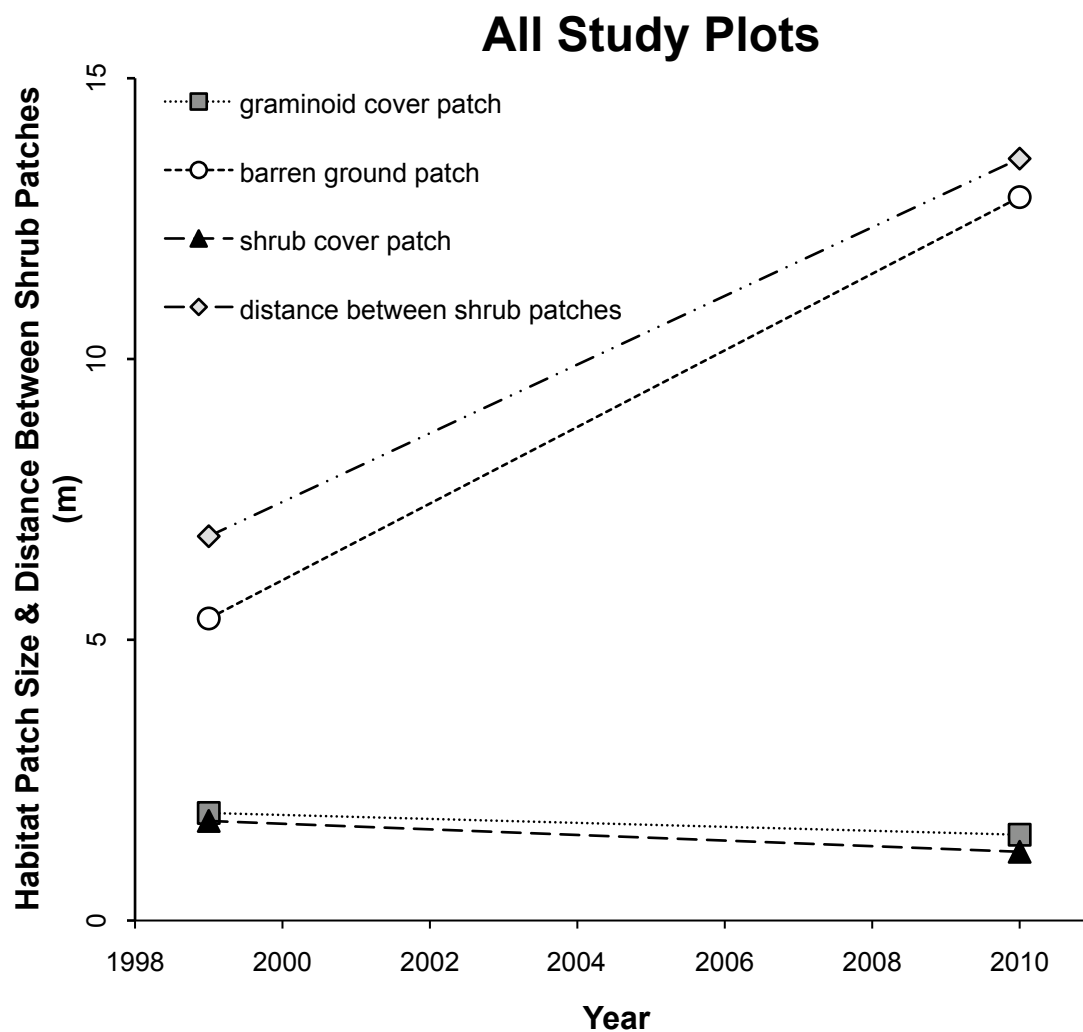


FIGURE 2.6. Patch size (m) estimates with trend line (95% confidence intervals not shown because of their small size relative to the symbol size; see Table 2.4 for precision) of habitat class (i.e. barren ground, graminoid cover, and shrub cover) patch size on all study plots, and distance between shrub patch estimates for 1999 and 2010.

Weatherhead Study Plot

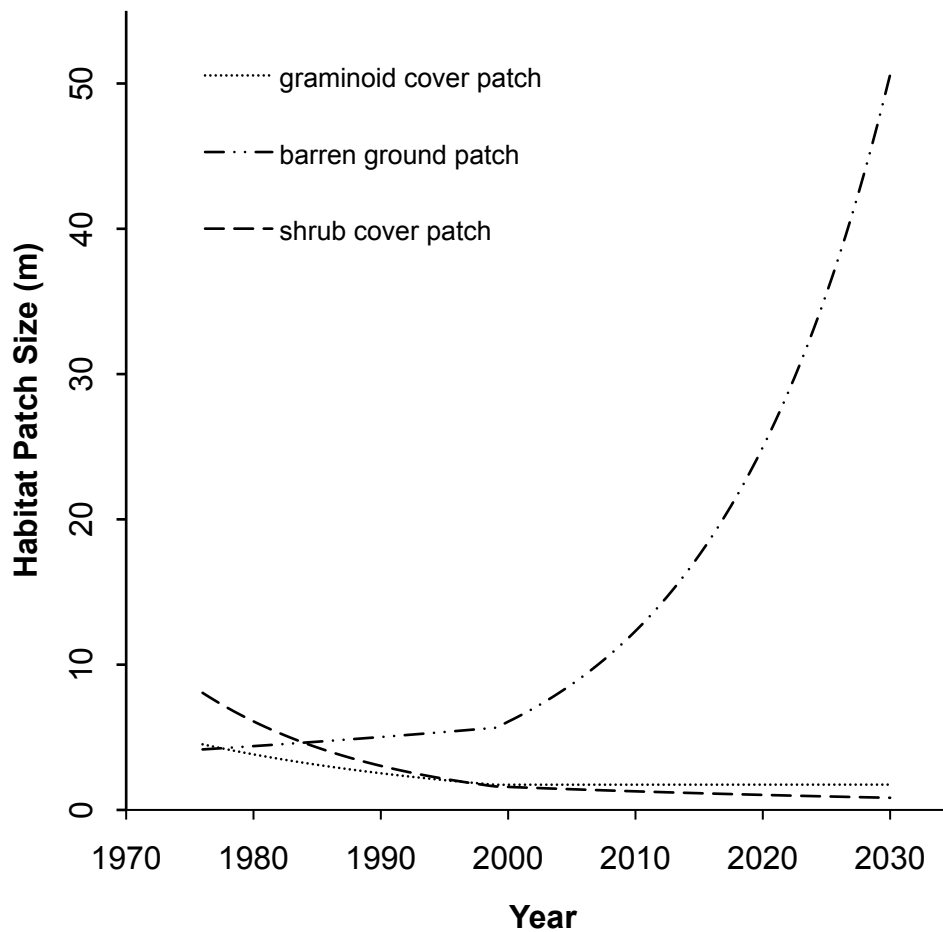


FIGURE 2.7. Historic (1976 – 2010) and future estimated (using 1999 – 2010 λ rate) annual geometric change in barren ground, graminoid and shrub cover patch size on the Weatherhead study plot.

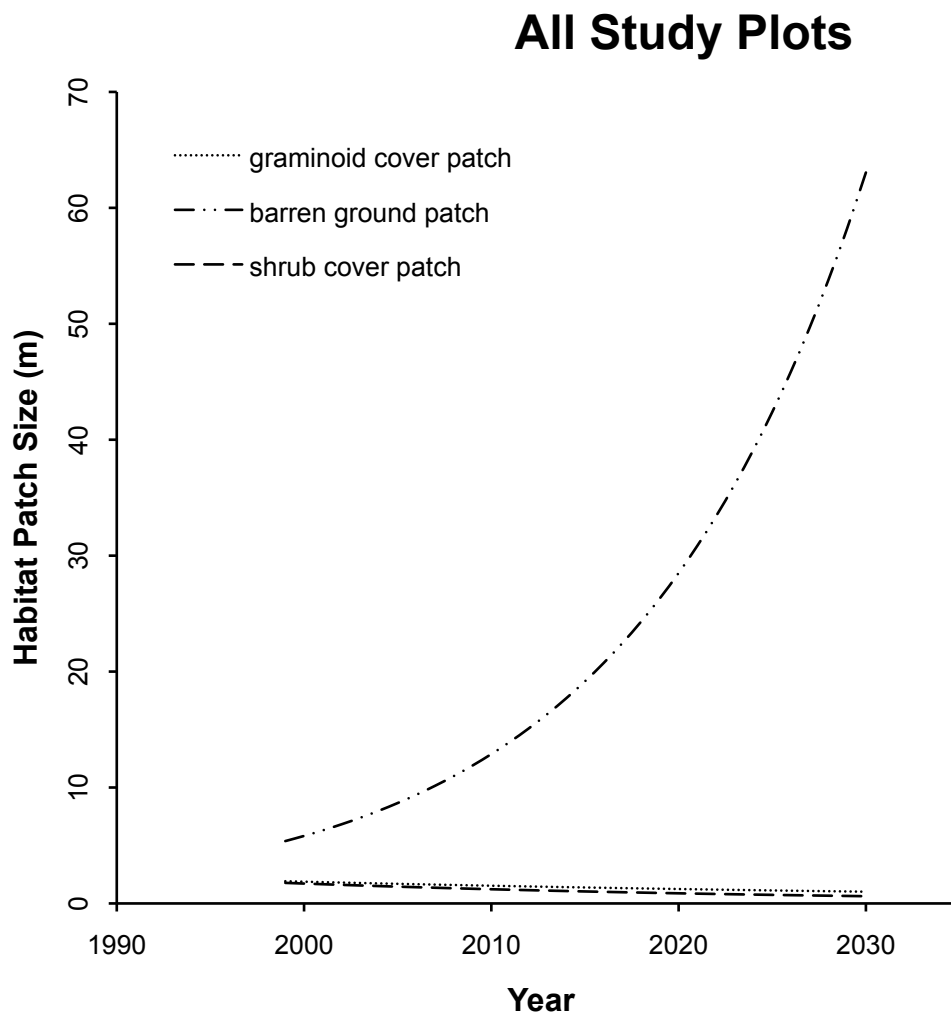


FIGURE 2.8. Historic (1999 – 2010) and future estimated annual geometric change in barren ground, graminoid and shrub cover patch size on all study plots.

Weatherhead Study Plot

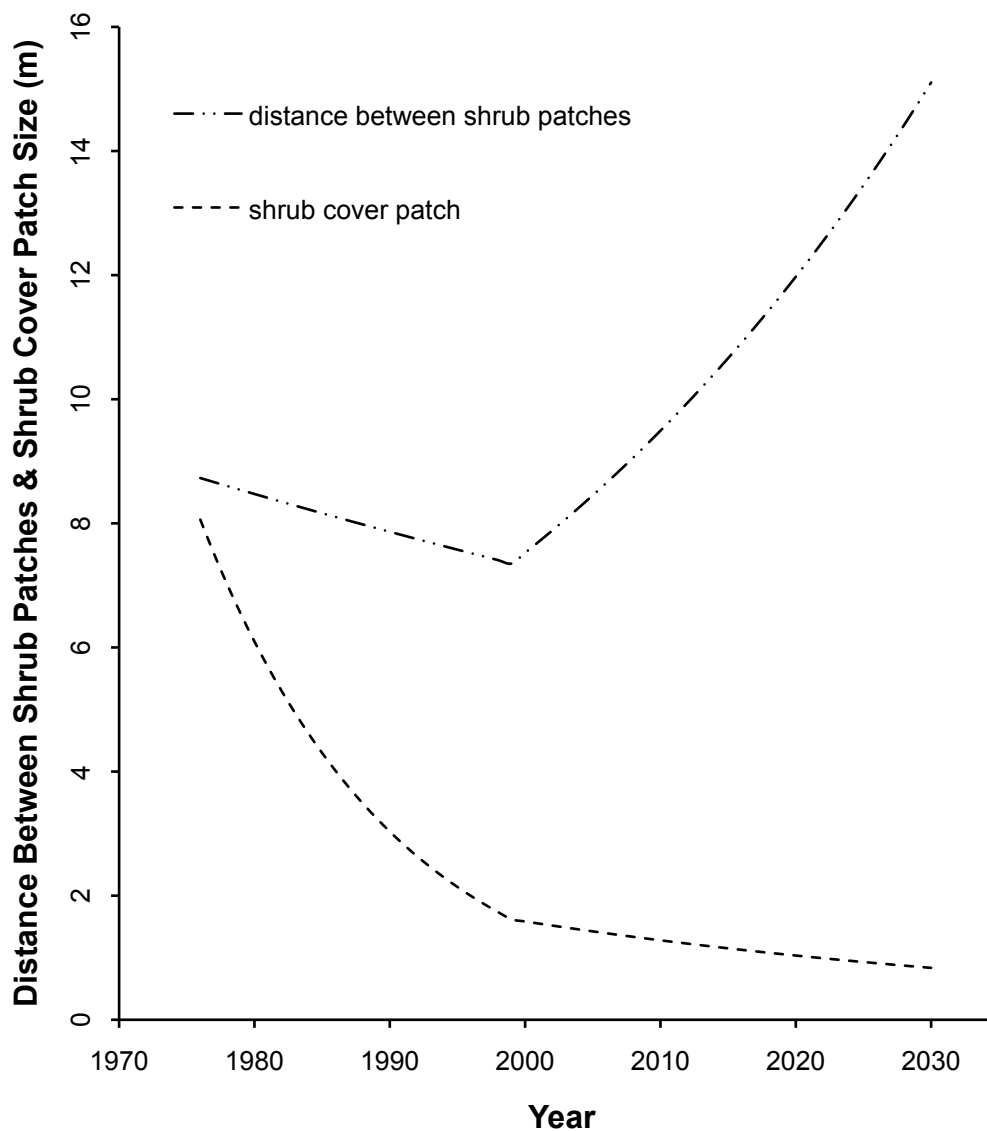


FIGURE 2.9. Historic (1976 – 2010) and future estimated (using 1999 – 2010 λ rate) annual geometric change in distance between shrub patches and shrub cover patch size on the Weatherhead study plot.

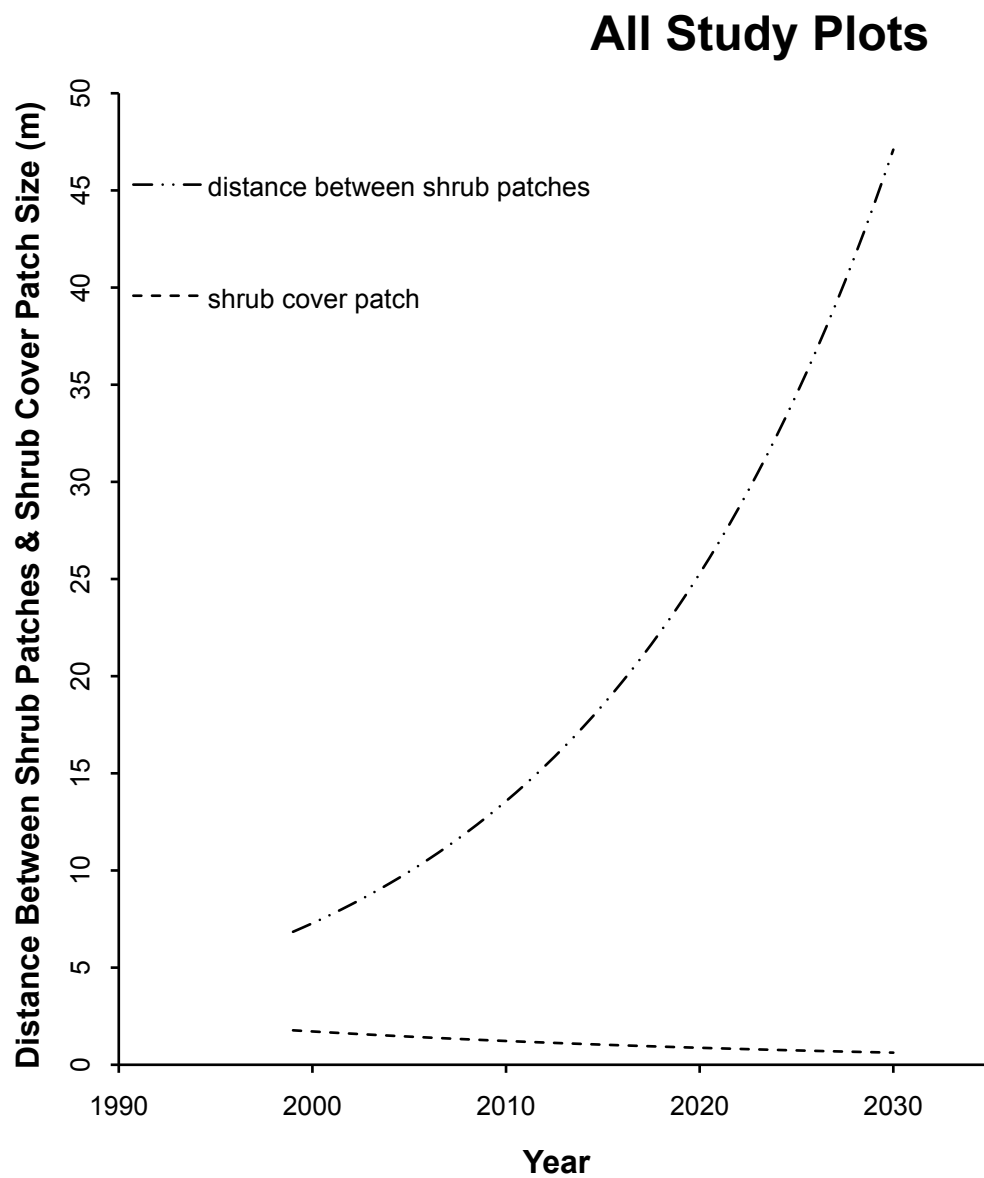


FIGURE 2.10. Historic (1999 – 2010) and future estimated annual geometric change in distance between shrub patches and shrub cover patch size on all study plots.

CHAPTER 3

IMPACTS OF LESSER SNOW GOOSE FORAGING ON THE OCCURRENCE OF
SAVANNAH SPARROW NESTING**Summary**

The mid-continent population of Lesser Snow Geese (*Chen caerulescens caerulescens*; LSGO) has increased 5-14% over the past 40 years. This has led to increased foraging and grubbing pressure by LSGO on their breeding and stopover sites along the Hudson Bay Lowlands in northern Canada. Degradation of these coastal salt-marsh and sedge meadow habitats are most evident at La Pérouse Bay. By examining the decline in vegetative cover and increasing areas of barren ground characterized by hyper-saline soils, researchers have identified not only alterations in the plant community and loss of plant species, but a decline in avian species assemblages that are dependent upon intact vegetative cover for foraging and nesting. In Chapter 2 we outlined in detail the loss of graminoid and shrub cover, and increases in barren ground, which have exacerbated the fragmentation of critical patches of habitat for ground-nesting birds.

In this chapter we use a multi-state occupancy model to investigate the impact that this loss in ground cover has had on Savannah Sparrow (*Passerculus sandwichensis*; SAVS) nesting occurrence at La Pérouse Bay. Although common across their northern range, local SAVS nest densities declined by 77% from 1976 to 1999. Adding to 1976 and 1999 nesting and spot mapping data, we surveyed the same study sites (total of 23 ha) in 2010 and 2011 and found an overall 10% annual decrease since 1999 in the probability of SAVS nesting occurrence at La Pérouse Bay. This precipitous decline in

nesting may be attributed to an increase in proportions of barren ground and the distance between patches of shrub cover habitat. In addition to habitat alterations, late spring and early summer temperatures (May and June) may also help to explain annual variation in occupancy rates of SAVS nesting.

Declines in local SAVS nesting occurrence at La Pérouse Bay may be indicative of the negative effects that expanding habitat degradation by LSGO may have on other ground-nesting avian species that share areas with LSGO along Arctic and sub-Arctic regions.

Introduction

Degradation of coastal salt-marsh and sedge meadow habitats due to increased foraging pressure by LSGO has been well documented over the past 35 years along the Hudson Bay Lowlands in Canada (Jefferies et al. 1979, Bazely and Jefferies 1986, Kerbes et al. 1990, Hik et al. 1992, Srivastava and Jefferies 1995, Jefferies and Rockwell 2002, Jefferies et al. 2006, Abraham et al. 2012). Chapter 2 outlines in detail the increased extent of barren ground and hypersaline soils at La Pérouse Bay specifically, with corresponding declines in both graminoid and shrub cover; further decreasing the size and quality of shrub habitat patches and foraging areas that are critical to a variety of ground-nesting avian species.

Recent declines of once common waterfowl in the La Pérouse Bay and surrounding Cape Churchill Peninsula region have been attributed to the degradation of habitat by LSGO. For example, Green-winged Teal (*Anas crecca*) and American Wigeon (*Anas americana*) numbers have decreased, perhaps because they depend on now-

degraded sedge and grass meadows as well as shrubs to conceal nests on the ground (Johnson 1995, Mowbray 1999, Rockwell et al. 2009). A census of birds in the region from 1968 to 1973 reported Long-tailed Ducks (*Clangula hyemalis*) as common migrants and summer residents with several nests located, but in 1982 there were only 14 nesting pairs of Long-tailed Ducks present, and only 1-2 pair accounted for from 1998 to 2000 (Cooke et al. 1975, Rockwell et al. 2009).

Declines in shorebird species in the area have been documented as well, which are dependent upon tall, dense swards of grasses and sedges for nesting. Proportional cover of these graminoid assemblages has decreased across the area, due to over-grazing by LSGO. For example, nesting pairs of Semipalmated Sandpipers (*Calidris pusilla*) declined by 16-18% per year between 1993 and 1999, and only one Red-necked Phalarope (*Phalaropus lobatus*) nest was observed annually since 1995, compared to more than 90 nests found in 1982 (Rockwell et al. 2009). The area is also used as a stopover site for many migrating shorebirds that forage on aquatic and terrestrial invertebrates, which they are dependent upon for much needed caloric energy during migration.

Examination of the degraded habitat sites at La Pérouse Bay has revealed not only alterations in the plant community and declines in avian populations, but also losses of important invertebrate species (Abraham et al. 2005). In particular, spider and ground beetle species have been lost in these degraded areas as well as the loss of species richness amongst midge communities, which may affect not only shorebirds but also nesting waterfowl and passerines in the area that utilize these invertebrates as a food resource (Milakovic et al. 2001, Milakovic and Jefferies 2003).

Habitat fragmentation, in particular, may have its strongest influence on ground-nesting passerines because it limits opportunities to find adequate nesting and foraging grounds. This in turn can affect their occurrence and reproductive success (Johnson 2001). Several studies have shown that habitat patch size has a significant influence on the occurrence of multiple sparrow species (Emberizidae family; Johnson and Temple 1986, 1990, Herkert 1994, Bollinger 1995, Johnson and Igl 2001). Johnson and Temple (1990) showed that SAVS nesting success was higher (i.e. less predation and parasitism) in larger patches of tallgrass prairie than in smaller patches of marginal habitat. In fact, SAVS were once common nesters in the La Pérouse Bay area, but by 1999 they had experienced a 77% reduction in average nesting densities in supratidal salt-marsh habitats relative to the 1970s when LSGO were less abundant and actually facilitated plant growth and habitat quality by contributing nitrogenous inputs to the soil through faecal matter (Weatherhead 1979, Rockwell et al. 2003, Abraham et al. 2012).

These observations of altered plant communities, and the decline of avian and invertebrate species at La Pérouse Bay, suggest that increased foraging by an expanding population of LSGO has led to a loss of habitat for multiple species. Using historical spot-mapping data of behavioral and physical evidence of nesting SAVS across 23 ha of degraded and marginally intact salt-marsh habitat, we assessed changes in SAVS nest numbers and examined the change in nesting occupancy rates (while accounting for detection probability) as it relates to changes in habitat conditions (refer to Chapter 2 for details). By using such an approach we reduce the bias that is associated with imperfect detection, and are able to more accurately understand the underlying environmental factors that may contribute to annual variation in the occurrence of SAVS nesting in

regions affected by LSGO foraging (MacKenzie et al. 2009). Although SAVS are known to be adaptable, robust breeders, we predict that the decline in vegetative cover caused by LSGO has been so severe that it has reduced the occurrence of SAVS nesting on the landscape.

Methods

Study Area

Study plots were located on coastal salt-marsh and shrub (supratidal) wetland habitat near La Pérouse Bay, approximately 30 kilometers east of Churchill, Manitoba, Canada (58° 52.3' N, 93° 41.0' W), which is part of the western Hudson Bay Lowlands and within the northern boundary of Canada's Wapusk National Park (Fig. 2.1).

Vegetation on the study area is characterized by dwarf shrub species (i.e. *Salix*, *Betula spp.*), salt-marsh grasses (e.g. *Puccinellia phryganodes*) and sedge species (e.g. *Carex subspathacea*) that LSGO prefer to forage on by grubbing and shoot pulling (Jefferies et al. 2003). With the increased foraging by LSGO on these graminoids, larger extents of hyper-saline soils have become more common throughout the general area. For further description of soil and vegetation interactions on the study area, see Iacobelli and Jefferies (1991), Srivastava and Jefferies (1995), and Jefferies and Rockwell (2002). For details on how LSGO have affected vegetation on the study area over time, see Chapter 2.

Study Species

The SAVS is a robust and adaptable ground nester, and although they have been considered as a habitat generalist throughout the majority of their range, their widespread

historical breeding on the study plots (Weatherhead 1979) makes them very good indicators of shrub habitat quality, where they use low-lying dwarf shrubs in place of tall grasses as nesting cover in the northern limit of their range (Wheelwright and Rising 2008).

Survey Plots

Nest searching for SAVS was conducted on five study plots, which were set up in a grid system of 50 m² cells and included portions of a study site established in 1976 (7 ha) to investigate the relationship between mating systems of SAVS and habitat quality (Weatherhead 1979). In addition to this plot, four paired study plots were established in 1999, representing heavily degraded habitats (2 plots, one of 3 ha and the other 5 ha) and marginally intact habitats (2 plots, one of 3 ha and the other 5 ha) that were geographically adjacent and representative of the habitats surrounding La Pérouse Bay.

All plots were re-established in 2010 by finding original northwest corners of each plot with GPS coordinates and then using wooden stakes, rebar poles, and flagging to establish corners of each 50 m² grid cell. Each cell was identified by a unique study plot name (i.e. Weatherhead, Close-to-Camp, Japanese Gardens) and an alpha-numeric system for identifying each grid cell. Grid cell columns ran north to south and were labeled with letters; rows ran east to west and were labeled with numbers (Fig. 2.2).

Nest searching was conducted in 1976 and 1977 on the Weatherhead study plot (Weatherhead 1979), and in 1999, 2000, 2010 and 2011 on all five study plots, a total of 92 grid cells. One to three observers thoroughly searched each grid cell for nests of all avian species every 5 to 7 days (every 2 days in 1976) by moving methodically from cell

to cell along each column. Any active nest, fresh nest bowl (current season only), or nest under construction was marked with a small uniquely labeled wooden stake, and recorded in a spot-mapping data book. A GPS point was taken for each nest in 2010 and 2011. Any breeding behavioral queues (i.e. aerial displays, singing males, contact and warning chip notes, mousing, broken wing display, etc.) of present avian species were also recorded and assisted observers in finding nests. Nests were also found by searching patches of shrub and grass cover suspected to have a nest under construction (as indicated in a previous survey) despite the absence of the species at the time of a given survey. All nests found were re-visited every 5 to 7 days to document nest activity and persistence. Survey periods started in the second or third week of June and ran until the third or fourth week in July. The number of sampling occasions was between 4 and 10 each year (5 in 1999; 10 in 2000; 4 in 2010; 5 in 2011). Yet, each year we continued to search for nests until no new nests were found on successive sampling occasions.

The objective of nest searches by Rockwell et al. (2003) was to evaluate how the loss in vegetative cover may have contributed to the decline of SAVS nests between 1976 and 1999 on the Weatherhead study plot. Our study objectives are similar to those of Rockwell et al. (2003). We report the change in SAVS nest numbers, but because of imperfect nest detection, we also model the change in nesting (breeding) occupancy rates across all study plots for 1999, 2000, 2010, and 2011.

Data Analysis

We initially attempted to model our detection history data by using a robust design multi-state occupancy model (MacKenzie et al. 2009) in Program MARK version

6.1, but could not obtain model convergence given the available data and the absence of occupancy data for the nine year period of 2001 to 2009.

We thus opted to use the single season, multi-state occupancy model to examine variation in nesting occupancy rates across all study plots over time, assuming that all grid cells were closed to occupancy changes over a given season (Nichols et al. 2007). Given the difficulty in finding ground-nesting passerine nests and the strong possibility that we did not find all SAVS nests present on the study plot, we considered three alternative states relevant to our objectives: a) no detection of nest or breeding activity (state = 0); b) detection of breeding behavior, which may include mousing (i.e. running on ground), broken wing display, copulation, incessant chipping (singing males not included, since some territories may be held with no attendant females present), repeated circling of entire cell, and carrying nesting material (state = 1); or c) detection of fresh nest bowl found with or without eggs, or partial nest bowl under construction within cell (state = 2). Under the multi-state occupancy framework, the lack of detecting a nest or breeding activity (state 0) does not necessarily imply that these activities were not present; the true state could be either one of the three states described above (state 0, 1, or 2). For example, if “breeding behavior” was detected, the true state could be 1 (e.g., in the breeding initiation phase) or a nest may have already been present (state 2), but we were unable to detect it. Only the highest ranking state (2: a nest was found) is unambiguous.

Use of these observations in the single season multi-state occupancy model allowed us to estimate: $\Psi^1 (\psi^1)$ = probability that a site was occupied by SAVS displaying breeding behavior that did or did not nest (true state = 1 or 2); $\Psi^2 (\psi^2)$ =

probability that nesting occurred at a site given that evidence of breeding was seen at the site (true state = 2 | true state = 1 or 2); p^1 = detection probability of occupancy given a true state of behavioral evidence; p^2 = probability of detecting nesting given that it occurred; and delta (δ) = probability that evidence of nesting was found given that breeding behavior was detected and nesting occurred, and accounts for the misclassification of the true state being 2.

We predicted that with the increase in barren ground and hyper-saline soils, which has led to a loss of ground and shrub cover (as detailed in Chapter 2), further fragmentation of suitable nesting habitat for SAVS would result in a decrease in nesting occupancy rates over time. Therefore, we examined four habitat class measurements and a single climate variable as explanatory covariates for the estimated occupancy parameters. The proportion of barren ground (covariate 1) was considered because snow goose foraging has led to an increase in barren ground over time, and a loss of ground cover with extended areas of hyper-saline soils. In turn, this has led to increased mortality of shrub assemblages and a decrease in the proportion of shrub cover (covariate 2) that SAVS depend upon for nesting cover. As shrub cover is lost, shrub patch size (covariate 3) decreases, which contributes to the loss of connectivity and increases the distance between suitable shrub habitat patches for nesting (covariate 4). We also examined the number of days above 0° C (covariate 5; using mean temperature of each day) in the months of May and June, which contributes to when available nesting habitat may open up for SAVS (i.e., become snow free and green up), and may additionally help explain annual variation of SAVS nesting occurrence on the landscape.

To compare models with alternative parameterizations of annual variation and covariate structures for the occupancy and detection parameters, we used Akaike's Information Criterion adjusted for sample size (AIC_c ; Akaike 1973). We used a bottom-up modeling approach beginning with a null model (no spatial or temporal variation in any parameter). Holding variation across sampling occasions constant, we proceeded by examining alternative forms of annual variation in p^1 , p^2 , and δ , one at a time, as well as the effects of the climate and spatio-temporal habitat covariates. After identifying the best model structure for the detection parameters, we modeled occupancy parameters (ψ^1 and ψ^2) as always being distinct from each other, and examined alternative models with each being time independent, time dependent, or with various additive and interactive combinations of the climate and spatio-temporal habitat covariates.

All models were run using the logit link function and the simulated annealing optimization routine, which is effective at finding the global maximum likelihood in multi-state data that may have multiple local maxima in the likelihood. Derived estimates of the unconditional probability that nesting occurred within one of the 92 grid cells was calculated as the product of the occupancy probabilities $\psi^{1*2} = \psi^1\psi^2$. Given that a grid cell equaled the average size of a SAVS nesting territory in the region (P. Weatherhead pers. comm.), ψ^{1*2} may also be interpreted as the expected proportion of potential SAVS territories where a nest was successfully built each year (Nichols et al. 2007, MacKenzie et al. 2010).

Results

SAVS Nest Numbers

Weatherhead Study Plot (1976 to 2011): In 1976 and 1977, observers located 24 and 14 SAVS nests respectively, across 28 grid cells (50 m²) in the Weatherhead study plot (7 ha). Search efforts were not as comprehensive in 1977 as they were in 1976 (Rockwell et al. 2003). Searching within the same 28 grid cells in 1999 and 2000, Rockwell et al. (2003) located only 6 and 4 SAVS nests, respectively. Search efforts on the Weatherhead study plot in 2010 and 2011 yielded 7 and 6 SAVS nests. Nest numbers were similar between the 1999-2000 and 2010-2011 period, which may suggest that the occurrence of SAVS nesting may have reached a stable state with what shrub habitat was available in 1999 and persisted over the ensuing 10-yr period, although nest numbers remained much lower than in the 1970s when habitat conditions were much better (see Chapter 2).

All Study Plots (1999 to 2011): Across all five study plots (92 grid cells; 23 ha) 31 SAVS nests were located in 1999 and 17 in 2000. In 2010 and 2011, we located a total of 13 nests each year, a decline by more than half since the 1999-2000 period.

Nest Occupancy Estimates

All Study Plots (1999, 2000, 2010, 2011): Our data supported a model with equivalent values of p^1 and p^2 in 1999, 2010, and 2011 ($p^1 = 0.16$, $p^2 = 0.88$), but lower probabilities of detection in 2000 ($p^1 = 0.03$, $p^2 = 0.56$) (Table 3.1). The probability of finding evidence of nesting, given detection of breeding behavior at a site where there was actually a nest to be found, was high in 1999 ($\delta = 0.99$), but somewhat lower in the

other years ($\delta = 0.90$ in 2000, 2010, and 2011). We found no support for effects of any of the climate and habitat covariates on the detection probabilities (the ΔAIC_c for models with covariate effects on the detection probabilities and other forms of annual variation were all > 75.0).

Using the most supported model structures for p^1 , p^2 , and δ presented above, we next modeled variation in the occupancy parameters (ψ^1 and ψ^2). The top model supported by AIC_c accounted for $\sim 60\%$ of the overall model weight, and indicated that the proportion of barren ground (bprop) in a grid cell was the best explanatory variable for variation in ψ^1 across the study area and over time (Table 3.2). Our top model also suggested that the distance between shrub patches (dist) and the number of days above 0° C (days > 0), treated as additive effects, were the best explanatory covariates for spatial and temporal variation in ψ^2 (Table 3.2). A second competing model structure with an overall model weight of $\sim 30\%$, indicated that additive effects between the proportion of barren ground and the number of days above 0° C (days > 0), and between the distance between shrub patches (dist) and the number of days above 0° C (days > 0) were all valid explanatory variables for the ψ^1 and ψ^2 estimates, respectively (Table 3.2). The estimates from this second model are practically identical to the estimates from our top model. We report our top model findings here. The average amount of barren ground across all study plots in 1999-2000 was 62%, compared to 78% in 2010-2011, which contributed to a decline in the average value of ψ^1 from 0.84 to 0.63 between these study periods (Table 3.1).

Our estimate for ψ^2 declined by more than half from 0.74 in 1999 to 0.30 in 2000 (Table 3.1). This annual variation may be explained by the fact that in 1999 there was 52

days above 0° C in May and June, which may have contributed to more snow free habitat and earlier green up of the vegetation, allowing for earlier nest initiation and building by SAVS. Multiple nests (with and without eggs) were found as early as June 10th. In 2000, there were 35 days above 0° C in May and June, and only one nest was found in the initiation phase (with no eggs and partially built) by June 17th.

We did not see a decline in ψ^2 between 2000 and 2010 suggesting that the occurrence of SAVS nesting had reached a stable state within the available habitat. The distance between shrub patches more than doubled from an average of 7.77 m in 1999 to 16.50 m in 2010 (refer to Chapter 2 for details), which contributed over time and space to lower probabilities of nesting occurrence across each grid cell (Fig. 3.1). This, along with annual climate variation (39 days > 0° C in 2010 and 33 days > 0° C in 2011), may best explain the decline in ψ^2 between 2010 and 2011 ($\psi^2 = 0.30$ in 2010, and 0.18 in 2011; Table 3.1, Fig. 3.1).

We evaluated derived estimates of unconditional probabilities of nesting occurring at a site (ψ^{1*2}) using the average covariate values for a given year across all study plots. These values of ψ^{1*2} declined from 0.62 in 1999 to 0.25 in 2000, 0.19 in 2010, and 0.12 in 2011 (Table 3.1, Figure 3.2).

Discussion

Over the past 35 years habitat degradation by LSGO has led to a significant loss of both graminoid and shrub cover assemblages; increasing the fragmentation of existing shrub habitat patches (Chapter 2). As predicted, we found that this has led to a decline in the occurrence of SAVS nesting across all study plots.

All SAVS nests that were found during the study were frequently associated with low-lying willow (*Salix spp.*), dwarf birch (*Betula glandulosa*), or sweet gale (*Myrica gale*) shrubs, and built right at the base of the shrub. This is contrary to habitat preferences of SAVS in more southern regions of their breeding range, where multiple studies have shown a negative relationship between the occurrence of SAVS and prevalence of woody vegetation (Ribic and Sample 2001, Bakker et al. 2002, Grant et al. 2004, Graves et al. 2010). What may be more important than the type of vegetation, is the structure of vegetation, which SAVS are more than likely queuing in on when selecting a nest site in northern regions of their breeding range where dwarf shrub species replace large extents of dense, tall grasses as the ideal habitat for concealing nests (Rottenberry and Knick 1999, Wheelwright and Rising 2008).

In 1976, La Pérouse Bay was bounded by a band of healthy and productive supratidal salt-marsh habitat with large patches of shrub habitat that supported nearly 3.44 SAVS nests per ha (Rockwell et al. 2003). Between 1976 and 1999 shrub cover declined at an annual rate of 5% ($\lambda = 0.95$; see Chapter 2), and by 1999 there were only an estimated 1.35 SAVS nests per ha (Rockwell et al. 2003). Shrub cover has continued to decline (6% annually since 1999; $\lambda = 0.94$; see Chapter 2), and by 2010 and 2011 there was only an average of 0.57 nests per ha.

Although we may be able to draw important inference on the number of nests found each year, one can never be certain if all nesting activity is detected (Nichols et al. 2007). Using multi-state occupancy models that account for imperfect detection and classification of breeding observations, we were able to explicitly examine how LSGO habitat degradation influenced SAVS nesting occurrence at La Pérouse Bay.

Although detection probabilities exhibited small amounts of variation across the study years, they were unrelated to any of the habitat variables (Table 3.1). Intuitively, one might expect that habitat cover would affect detection of nesting or breeding activity (i.e. less vegetative cover = higher detection rates, and vice-versa). In such a low-lying, sparsely covered habitat, detection of passerine species may not be as variable as in a more heterogeneous environment with larger extents of grass and shrub cover, and taller willow (*Salix spp.*) shrubs.

Breeding distribution and microhabitat (i.e. nest site) selection among various ground-nesting avian species has been shown to be influenced by biotic (e.g. habitat composition) and abiotic (e.g. climate conditions) variation (Gratto and Cooke 1987, Morton 1994, Martin 2001, Hendricks 2003, Martin et al. 2009). These same processes may influence the annual propensity of SAVS nesting effort. For example, we found that both habitat composition (i.e. barren ground proportion, distance between shrub patch habitats) and annual variation in temperature (number of days $> 0^{\circ}\text{C}$ in May and June) were contributing factors to declines in SAVS nesting occurrence across our study site. Habitat alteration may contribute to more long-term declines in the occurrence of SAVS nesting, whereas annual variation in temperature and other possible climate related variables may influence short-term fluctuations in the propensity of SAVS nesting.

Over a 10-yr period, behavioral evidence (ψ^1) of SAVS nesting activity declined by 3% per year ($\lambda = 0.97$) across the study area (Table 3.1). This was best explained by a 2% annual increase ($\lambda = 1.02$) in the proportion of barren ground (refer to Chapter 2 for details). The increase in the proportion of barren ground was associated with the loss of

quality nesting and foraging habitat, thereby reducing the number of SAVS utilizing the area.

Extended areas of barren ground were not homogenous, but were associated with increased fragmentation of shrub habitat patches, which more than doubled over the same period (refer to Chapter 2 for details). This increase in distance between shrub habitat patches along with the annual variation in the number of days above 0° C in May and June best explained the precipitous decline (8% annually; $\lambda = 0.92$) in SAVS nesting (ψ^2) across the study site (Table 3.1).

It is important to note that between 1999 and 2000, the conditional probability of SAVS nesting (ψ^2) across our study site decreased significantly from 0.74 to 0.30 (Table 3.1), reflective of the highly unpredictable annual climate along western Hudson Bay. In 1999, there were 52 days with temperatures above 0° C in May and June, an unusually warm year, but only 35 days above 0° C in May and June of 2000, slightly below a 13 year average of 42 days above 0° C in May and June (Fig. 3.3). This annual variation in temperature may moderate the amount of habitat that is actually available for migrant SAVS arriving on their breeding grounds, and dictate when males may be able to establish territories. By taking into account the annual variation in late spring temperatures along with barren ground proportion increases of 20%, and an increased distance of 6.73 m between shrub patch habitats, derived estimates of the expected proportion (ψ^{1*2}) of potential SAVS territories with successful nesting declined annually by 10% ($\lambda = 0.90$) over a ten year period (Table 3.1, Fig. 3.2).

The consequences of further habitat degradation by LSGO will not only impact nesting SAVS, but will also negatively affect other passerines that are less adaptable and

robust than SAVS. Associated declines in abundance of Arctic and sub-Arctic avian species could lead to a greater number of species being listed as threatened or endangered, and if enough species are affected, a loss of biodiversity. These issues will need to be addressed by resource managers on the Canadian breeding grounds, as well as along migratory pathways in the central United States.

Our study provides insight into ways that natural resource managers may be able to mitigate habitat degradation and trophic impacts on species diversity and richness. We recommend incorporating our frameworks for modeling habitat (Chapter 2) and avian breeding occurrence (this chapter) into local and regional monitoring efforts of Arctic and sub-Arctic habitats and those avian communities that utilize them. This will assist managers in estimating long-term trends in the persistence of breeding SAVS and other similar ground-nesting bird species that share habitats with over-abundant LSGO along the Hudson Bay Lowlands and the high Arctic areas where LSGO populations are rapidly growing (Kerbes et al. 1990).

References

- Abraham, K. F., R. L. Jefferies, and R. T. Alisauskas. 2005. The dynamics of landscape change and snow geese in mid-continent North America. *Global Change Biology* 11:841-855.
- Abraham, K. F., R. L. Jefferies, R. T. Alisauskas, and R. F. Rockwell. 2012. Northern wetland ecosystems and their response to high densities of Lesser Snow Geese and Ross's Geese. Pages 9-45 *in* Evaluation of Special Management Measures for Midcontinent Lesser Snow Geese and Ross's Geese (J. O. Leafloor, T. J. Moser,

and B. D. J. Batt, Eds.). Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service, Washington, D.C. and Canadian Wildlife Service, Ottawa, Ontario.

Akaike, H., 1973. Information theory and an extension of the maximum likelihood principle. Pages 267–281 in 2nd International Symposium on Information Theory (B. N. Petran and F. Csaki, Eds.). Akademiai Kiado, Budapest, Hungary.

Bakker, K. K., D. E. Naugle, and K. F. Higgins. 2002. Incorporating landscape attributes into models for migratory grassland bird conservation. *Conservation Biology* 16:1638-1646.

Bazely, D. R., and R. L. Jefferies. 1986. Changes in the composition and standing crop of salt-marsh communities in response to the removal of a grazer. *The Journal of Ecology*, 74:693–706.

Bollinger, E. K. 1995. Successional changes and habitat selection in hayfield bird communities. *Auk* 112:720-30.

Cooke, F., R. K. Ross, R. K. Schmidt, and A. J. Pakulak. 1975. Birds of the tundra biome of Cape Churchill and La Pérouse Bay. *Canadian Field Naturalist* 89:413-422.

Grant, T. A., E. Madden, and G. B. Berkey. 2004. Tree and shrub invasion in northern mixed-grass prairie: implications for breeding grassland birds. *Wildlife Society Bulletin* 32:807-818.

Gratto, C. L., and F. Cooke. 1987. Geographic variation in the breeding biology of the Semipalmated Sandpiper. *Ornis Scandinavica* 18:233-235.

- Graves, B. M., A. D. Rodewald, and S. D. Hull. 2010. Influence of woody vegetation on grassland birds within reclaimed surface mines. *Wilson Journal of Ornithology* 122:646-654.
- Hendricks, P. 2003. Spring snow conditions, laying date, and clutch size in an alpine population of American Pipits. *Journal of Field Ornithology* 74:423-429.
- Herkert, J. R. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. *Ecological Applications* 4:461-471.
- Hik, D. R., R. L. Jefferies, and A. R. E. Sinclair. 1992. Foraging by geese, isostatic uplift and asymmetry in the development of salt-marsh plant communities. *Journal of Ecology* 80:395-406.
- Iacobelli, A., and R. L. Jefferies. 1991. Inverse salinity gradients in coastal marshes and the death of *Salix*; the effects of grubbing by geese. *Journal of Ecology* 79:61-73.
- Jefferies, R. L., A. Jensen, and K. F. Abraham. 1979. Vegetational development and the effect of geese on vegetation at La Pérouse Bay, Manitoba. *Canadian Journal of Botany* 57:1439-1450.
- Jefferies, R. L., and R. F. Rockwell. 2002. Foraging geese, vegetation loss and soil degradation in an Arctic salt marsh. *Applied Vegetation Science* 5:7-16.
- Jefferies, R. L., R. F. Rockwell, and K. F. Abraham. 2003. The embarrassment of riches: Agricultural food subsidies, high goose numbers and loss of Arctic wetlands – a continuing saga. *Environmental Review* (Natural Resource Council Canada) 11:193-232.

- Jefferies, R. L., A. P. Jano, and K. F. Abraham. 2006. A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology* 94:234–242.
- Johnson, R. G., and S. A. Temple. 1986. Assessing habitat quality for birds nesting in fragmented tallgrass prairies. Pages 245–249 *in* *Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates* (J. Verner, M. L. Morrison, and C. J. Ralph, Eds.). Madison: University of Wisconsin Press.
- Johnson, R. G., and S. A. Temple. 1990. Nest predation and brood parasitism of tallgrass prairie birds. *Journal of Wildlife Management* 54:106–111.
- Johnson, D. 2001. Habitat fragmentation effects on birds in grasslands and wetlands: a critique of our knowledge. *Great Plains Research: A Journal of Natural and Social Sciences*. Paper 568. <http://digitalcommons.unl.edu/greatplainsresearch/568>.
- Johnson, D. H., and L. D. Igl. 2001. Area requirements of grassland birds: A regional perspective. *Auk* 118:24–34.
- Johnson, K. 1995. Green-winged Teal (*Anas crecca*). *In* *The Birds of North America*, no. 193 (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/193>.
- Kerbes, R. H., P. M. Kotanen, and R. L. Jefferies. 1990. Destruction of wetland habitats by lesser snow geese: A keystone species on the west coast of Hudson Bay. *Journal of Applied Ecology* 27:242–258.
- MacKenzie, D. I., J. D. Nichols, M. E. Seamons, and R. J. Gutiérrez. 2009. Modeling species occurrence dynamics with multiple states and imperfect detection. *Ecology* 90:823–835.

- MacKenzie, D. I., M. E. Seamons, R. J. Gutiérrez, and J. D. Nichols. 2010. Investigating the population dynamics of California Spotted Owls without marked individuals. *Journal of Ornithology* 152:597-604.
- Martin, M., A. F. Camfield, and K. Martin. 2009. Demography of an alpine population of Savannah Sparrows. *Journal of Field Ornithology* 80:253-264.
- Martin, T. E. 2001. Abiotic vs. biotic influences on habitat selection of coexisting species: Climate change impacts? *Ecology* 82:175-188.
- Milakovic B., T. J. Carleton, and R. L. Jefferies. 2001. Changes in midge (Diptera: Chironomidae) populations of sub-arctic supratidal vernal ponds in response to goose foraging. *Ecoscience* 8:58-67.
- Milakovic B., and R. L. Jefferies. 2003. The effects of goose herbivory and loss of vegetation on ground beetle and spider assemblages in an Arctic supratidal marsh. *Ecoscience* 10:57-65.
- Morton, M. 1994. Comparison of reproductive timing to snow conditions in wild onions and White-crowned Sparrows at high altitude. *Great Basin Naturalist* 54:371-375
- Mowbray, T. 1999. American Wigeon (*Anas americana*). In *The Birds of North America*, no. 401 (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/401>.
- Nichols, J. D., J. E. Hines, D. I. Mackenzie, M. E. Seamans, and R. J. Gutiérrez. 2007. Occupancy estimation and modeling with multiple states and state uncertainty. *Ecology* 88:1395-400.
- Ribic, C. A., and D. W. Sample. 2001. Associations of grassland birds with landscape factors in southern Wisconsin. *The American Midland Naturalist* 146:105-121.

- Rockwell, R. F., C. R. Witte, R. L. Jefferies, and P. J. Weatherhead. 2003. Response of nesting Savannah Sparrows to 25 years of habitat change in a Snow Goose colony. *Ecoscience* 10:33-37.
- Rockwell, R. F., K. F. Abraham, C. R. Witte, P. Matulonis, M. Usai, D. Larsen, F. Cooke, D. Pollak, and R. L. Jefferies. 2009. The Birds of Wapusk National Park. Wapusk National Park of Canada Occasional Paper #1. Winnipeg, Manitoba. Parks Canada.
- Rotenberry, J. T., and S. T. Knick. 1999. Multiscale habitat associations of the Sage Sparrow: Implications for conservation biology. *Studies in Avian Biology* 19:95–103.
- Srivastava, D. S., and R. L. Jefferies. 1995. Mosaics of vegetation and soil salinity: a consequence of goose foraging in an arctic salt marsh. *Canadian Journal of Botany* 73:75-83.
- Weatherhead, P. J. 1979. Ecological correlates of monogamy in tundra-breeding Savannah Sparrows. *Auk* 96:391-401.
- Wheelwright, N. T., and J. D. Rising. 2008. Savannah Sparrow (*Passerculus sandwichensis*). In *The Birds of North America*, no. 45 (A. Poole, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America Online: <http://bna.birds.cornell.edu/bna/species/045>.

TABLE 3.1. Parameter estimates for the top single season, multi-state occupancy model for surveyed grid cells ($n = 92$) at La Pérouse Bay, Manitoba, Canada in the summers of 1999, 2000, 2010, and 2011. Occupancy parameter estimates were evaluated at the number of days above 0° C in May and June of each year, and the average values of the proportion of barren ground and distance between shrub habitat patches (m) for each year.

Parameter	1999		2000		2010		2011	
	Est	SE	Est	SE	Est	SE	Est	SE
ψ^1	0.84	0.070	0.84	0.070	0.63	0.071	0.63	0.071
ψ^2	0.74	0.070	0.30	0.044	0.30	0.055	0.18	0.041
ψ^{1*2}	0.62	0.051	0.25	0.034	0.19	0.031	0.12	0.025
p^1	0.16	0.027	0.03	0.009	0.16	0.027	0.16	0.027
p^2	0.88	0.017	0.56	0.032	0.88	0.017	0.88	0.017
δ	0.99	0.007	0.90	0.019	0.90	0.019	0.90	0.019

Definition of parameters: ψ^1 = probability that a site was occupied by SAVS displaying breeding behavior that did or did not nest (true state = 1 or 2); ψ^2 = probability that nesting occurred at a site given that evidence of breeding was seen at the site (true state = 2 | true state = 1 or 2); ψ^{1*2} = the unconditional probability of SAVS nesting occurrence or the expected proportion of potential SAVS territories where a nest was successfully built each year; p^1 = detection probability of occupancy given a true state of behavioral evidence; p^2 = probability of detecting nesting given that it occurred; and delta (δ) = probability that evidence of nesting was found given that breeding behavior was detected and nesting occurred, and accounts for the misclassification of the true state being 2.

TABLE 3.2. Comparison of the top 10 single season, multi-state occupancy models for surveyed grid cells ($n = 92$) at La Pérouse Bay, Manitoba, Canada in the summer of 1999, 2000, 2010, and 2011.

Model	N	ΔAIC_c	w
ψ^1 (bprop), ψ^2 (dist + days > 0), $[p^1, p^2]$ (00, .), $[\delta]$ (99, .)	11	0	0.60
ψ^1 (bprop + days > 0), ψ^2 (dist + days > 0), $[p^1, p^2]$ (00, .), $[\delta]$ (99, .)	12	1.42	0.30
ψ^1 (bprop*days > 0), ψ^2 (dist + days > 0), $[p^1, p^2]$ (00, .), $[\delta]$ (99, .)	12	3.54	0.10
ψ^1 (dist), ψ^2 (dist + days > 0), $[p^1, p^2]$ (00, .), $[\delta]$ (99, .)	11	11.38	< 0.01
ψ^1 (sprop), ψ^2 (dist + days > 0), $[p^1, p^2]$ (00, .), $[\delta]$ (99, .)	11	14.94	< 0.01
ψ^1 (bpatch), ψ^2 (dist + days > 0), $[p^1, p^2]$ (00, .), $[\delta]$ (99, .)	11	16.15	< 0.01
ψ^1 (.), ψ^2 (dist + days > 0), $[p^1, p^2]$ (00, .), $[\delta]$ (99, .)	10	18.86	< 0.01
ψ^1 (.), ψ^2 (sprop + days > 0), $[p^1, p^2]$ (00, .), $[\delta]$ (99, .)	10	20.77	< 0.01
ψ^1 (.), ψ^2 (yr), $[p^1, p^2]$ (00, .), $[\delta]$ (99, .)	11	20.78	< 0.01
ψ^1 (spatch), ψ^2 (dist + days > 0), $[p^1, p^2]$ (00, .), $[\delta]$ (99, .)	11	20.80	< 0.01

Variables considered in these *a priori* models were proportion of barren ground (bprop), proportion of shrub cover (sprop), barren ground patch size (bpatch), shrub patch size (spatch), distance between shrub patches (dist), and number of days above 0° C (days > 0) in May and June. Parameters p^1 and p^2 were modeled as different only in 2000 relative to 1999, 2010, and 2011 (00, .). Parameter δ was modeled as different only in 1999 relative to 2000, 2010, and 2011 (99, .). N is the number of beta parameters estimated. ΔAIC_c is the relative difference in AIC_c values compared to the top-ranked model. w is the contributed AIC_c weight to the model.

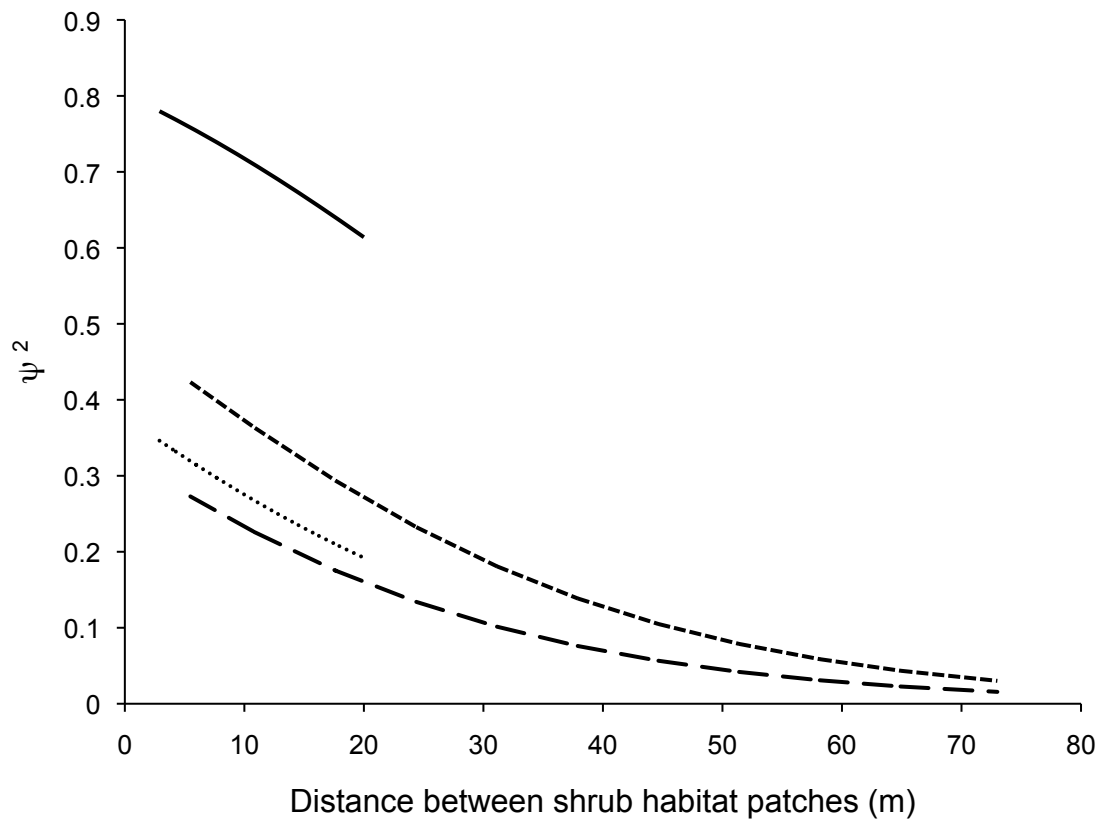


FIG. 3.1. Estimated probabilities of nesting occurring, given site occupancy by birds that were at least displaying behavioral evidence (ψ^2) in relation to distance between patches of shrub habitat at a site in 1999 (solid line), 2000 (dotted line), 2010 (short dashed line) and 2011 (long dashed line) evaluated at the number of days above 0° C in May and June of each year. All lines extend across the range of observed values of the independent variable in each year.

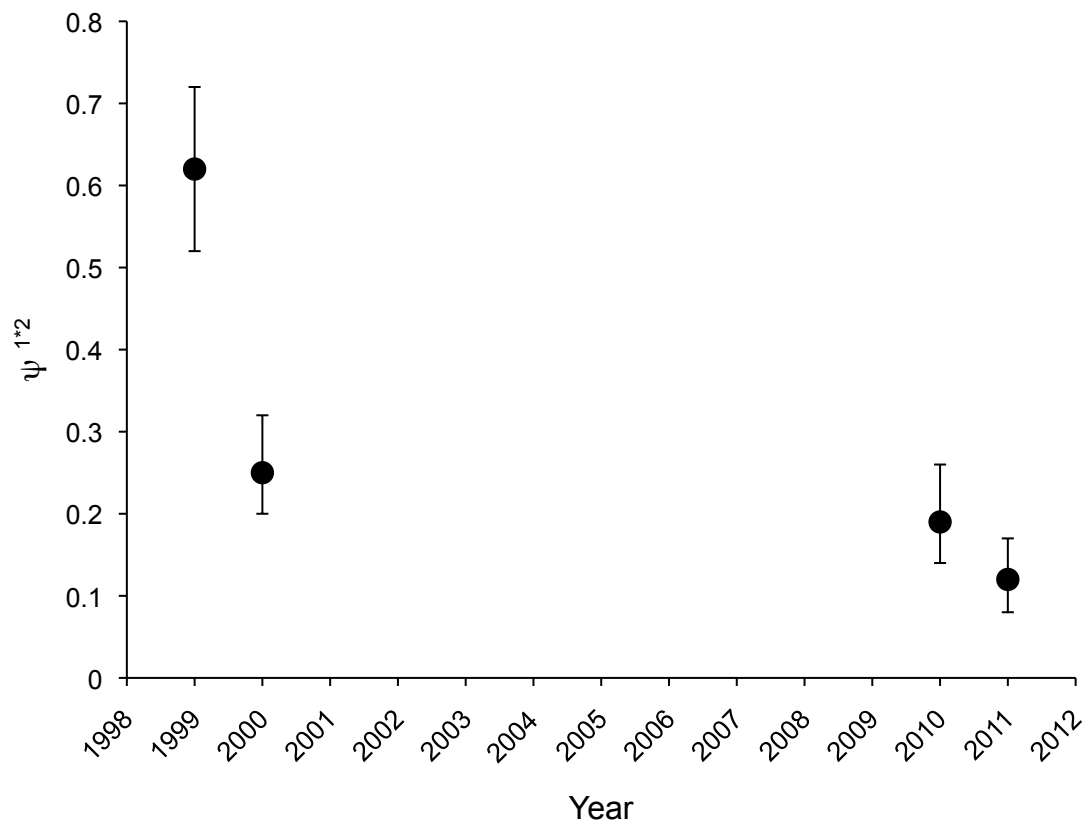


FIG. 3.2. Derived estimates of the unconditional probability (ψ^{1*2}) that nesting occurred within one of the surveyed grid cells (1999, 2000, 2010, and 2011). 95% confidence intervals are illustrated with the bars around each estimate of the mean value (dots).

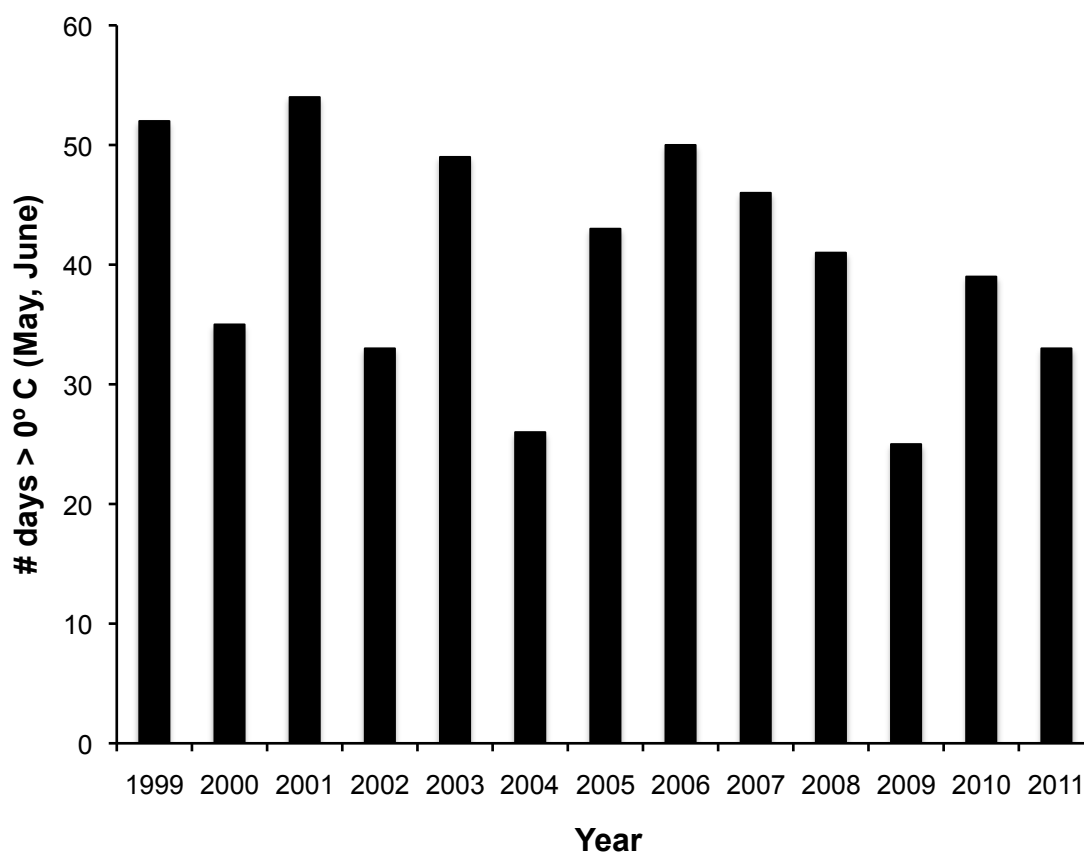


FIG. 3.3. A 13 year period showing the number of days $> 0^{\circ}\text{C}$ (based on mean daily temperature) in May and June in the Churchill, Manitoba, Canada area.

CHAPTER 4

CONCLUSIONS

Researchers have recently observed a human-induced terrestrial trophic cascade along the Hudson Bay lowlands of northern Manitoba, Canada, where modified landscapes in one region have led to drastically altered ecosystems and species assemblages in a distant ecosystem (Milakovic et al. 2001, Milakovic and Jefferies 2003, Rockwell et al. 2003, Jefferies et al. 2004, Abraham et al. 2005*b*). Increased foraging and grubbing pressure by an expanding population of Lesser Snow Geese (*Chen caerulescens caerulescens*; LSGO) on supratidal marsh habitats of La Pérouse Bay have led to increased barren ground, hypersaline soils, and significant declines in graminoid and shrub cover (refer to Chapter 2 for details; Iacobelli and Jefferies 1991, Jefferies and Rockwell 2002, Abraham et al. 2005*a*).

This habitat degradation has shifted a once healthy supratidal salt-marsh ecosystem into an alternative state which holds little to no value for ground-nesting avian species that rely on intact patches of graminoid and shrub cover habitat. Local population declines in waterfowl, shorebird and passerine species have been observed over the past 35 years at La Pérouse Bay (Rockwell et al. 2009). In particular, nesting occurrence of the readily adaptable ground-nesting Savannah Sparrow (*Passerculus sandwichensis*; SAVS) has declined precipitously due to an extensive loss of shrub cover (i.e. *Salix spp.*, *Betula glandulosa*, *Myrica gale*) and the continuing fragmentation of patches of shrub habitat (refer to Chapter 3 for details; Rockwell et al. 2003).

In Chapter 2, we continued the assessment of the ongoing alteration of vegetation assemblages and habitat quality over a 35-yr period by estimating proportional changes in 3 habitat classes (barren ground, graminoid and shrub cover); changes in the patch size of each habitat class; and the distance between shrub cover patches, which provided insight into the level of habitat fragmentation.

Despite the movement of most LSGO to other areas in the region, we found that their legacy continues to deteriorate the habitat via abiotic processes set into motion by the geese (Kerbes et al. 1990, Hik et al. 1992, Srivastava and Jefferies 1995, Jefferies and Rockwell 2002, Jefferies et al. 2006). The shrub cover assemblage declined most abruptly over time across the entire study area. This loss in shrub cover was facilitated by significant increases in the proportion and patch size of barren ground, which subsequently increases soil water salinity and limits re-colonization by shrub and graminoid assemblages. Additionally, with an increase in the extent of barren ground, the connectivity of shrub cover was lost, which could negatively affect the breeding success of many ground-nesting birds in the study area, including SAVS.

In Chapter 3, we assessed changes in SAVS nest numbers and examined the change in nesting occupancy rates as it relates to changes in habitat conditions that we elucidated in Chapter 2. We developed a multi-state occupancy model (which accounts for detection probability) using behavioral and physical evidence of nesting collected on the same study area as the vegetation surveys examined in Chapter 2.

Nest numbers of SAVS decreased by > 50% over the entire study period, due to precipitous declines in shrub cover across the study area. We also found a reduction in the number of breeding SAVS utilizing the area, which was associated with the loss of

quality nesting and foraging habitat due to an increase in the proportion of barren ground. As barren ground increased, the distance between patches of shrub habitat increased, leading to further fragmentation of quality nesting areas for SAVS. Along with annual variation in late spring temperatures, distance between shrub patches contributed to an annual decrease of 8% in the probability of SAVS nesting.

Although the highly unpredictable climate along the western Hudson Bay lowlands may moderate the amount of habitat that is actually available for migrant SAVS arriving on their breeding grounds, and dictate when males may be able to establish territories, the strongest explanatory variable for long-term breeding success may be the distance between patches of shrub habitat.

In 1999 only 33% of all surveyed grid cells (i.e. SAVS territories) across the study site were unoccupied (no breeding behavioral or physical evidence), compared to almost 60% of grid cells in 2000, which were absent of any nesting evidence. In 2010 and 2011, almost 60% of all grid cells held no evidence of nesting, which is comparable to the 2000 season, but there were 23 replicate grid cells in 1999 – 2000 which were always unoccupied, compared to 55 grid cells in 2010 – 2011 that were always unoccupied. Concurrently, the distance between patches of shrub habitat in the unoccupied grid cells doubled over a 10-yr period from 9.29 m to 18.74 m. Although these naïve occupancy estimates do not take into account imperfect detection, it does illustrate how the loss in connectivity of quality habitats can have negative consequences on the breeding success of SAVS and other similar ground-nesting avian species. The formal occupancy analyses that accounted for imperfect detection confirmed these observations.

If the observed change in habitat continues at the rates most recently observed (refer to Chapter 2 for details), shrub patches may be reduced to less than 1 m in size by 2017 with exponential increases in the distance between patches further fragmenting any viable habitat connectivity (Fig. 2.8). Although these alterations in habitat may be strongly associated with declines in avian species assemblages at a local level, strong inference at regional scales has not been found (Sammler et al. 2008). However, continued monitoring of these habitat changes at decadal intervals is recommended in order to help establish threshold and stability properties of habitat change originally induced by LSGO foraging pressure (Rumpff et al. 2011), and continued monitoring of ground-nesting passerines in areas they share with LSGO would provide insight into ways that natural resource managers may be able to mitigate habitat degradation and trophic impacts on species diversity and richness.

We concur with the recommendations of Abraham et al. (2012) that assessment of vegetation changes and potential for recovery along the western coast of Hudson Bay should be continued, and that identifying areas with the highest potential for LSGO growth may help us to estimate the spatial carrying capacity for LSGO. This may assist managers in judging the full extent to which Arctic and sub-Arctic ecosystems might be vulnerable to LSGO degradation.

To assist managers in estimating long-term trends in ground-nesting avian species that share habitat with LSGO, we recommend incorporating our frameworks for modeling habitat (Chapter 2) and avian breeding occurrence (Chapter 3) into local and regional monitoring efforts of Arctic and sub-Arctic habitats and those avian communities that utilize them.

References

- Abraham, K. F., R. L. Jefferies, and R. F. Rockwell. 2005*a*. Goose-induced changes in vegetation and land cover between 1976 and 1997 in an Arctic coastal marsh. *Arctic, Antarctic, and Alpine Research* 37:269-275.
- Abraham, K. F., R. L. Jefferies, and R. T. Alisauskas. 2005*b*. The dynamics of landscape change and Snow Geese in mid-continent North America. *Global Change Biology* 11:841-855.
- Abraham, K. F., R. L. Jefferies, R. T. Alisauskas, and R. F. Rockwell. 2012. Northern wetland ecosystems and their response to high densities of Lesser Snow Geese and Ross's Geese. Pages 9-45 *in* Evaluation of Special Management Measures for Midcontinent Lesser Snow Geese and Ross's Geese. (J. O. Leafloor, T. J. Moser, and B. D. J. Batt, Eds.). Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service, Washington, D.C. and Canadian Wildlife Service, Ottawa, Ontario.
- Hik, D. R., R. L. Jefferies, and A. R. E. Sinclair. 1992. Foraging by geese, isostatic uplift and asymmetry in the development of salt-marsh plant communities. *Journal of Ecology* 80:395-406.
- Iacobelli, A., and R. L. Jefferies. 1991. Inverse salinity gradients in coastal marshes and the death of *Salix*; the effects of grubbing by geese. *Journal of Ecology* 79:61-73.
- Jefferies, R. L., and R. F. Rockwell. 2002. Foraging geese, vegetation loss and soil degradation in an Arctic salt marsh. *Applied Vegetation Science* 5:7-16.

- Jefferies, R. L., R. F. Rockwell, and K. F. Abraham. 2004. Agricultural food subsidies, migratory connectivity and large-scale disturbance in arctic coastal systems: A case study. *Integrative and comparative biology* 44:130-9.
- Jefferies, R. L., A. P. Jano, and K. F. Abraham. 2006. A biotic agent promotes large-scale catastrophic change in the coastal marshes of Hudson Bay. *Journal of Ecology* 94: 234-242.
- Kerbes, R. H., P. M. Kotanen, and R. L. Jefferies. 1990. Destruction of wetland habitats by Lesser Snow Geese: A keystone species on the west coast of Hudson Bay. *Journal of Applied Ecology* 27:242–258.
- Milakovic, B., T. J. Carleton, and R. L. Jefferies. 2001. Changes in midge (Diptera: Chironomidae) populations of sub-arctic supratidal vernal ponds in response to goose foraging. *Ecoscience* 8:58–67.
- Milakovic, B., and R. L. Jefferies. 2003. The effects of goose herbivory and loss of vegetation on ground beetle and spider assemblages in an Arctic supratidal marsh. *Ecoscience* 10:57–65.
- Rockwell, R. F., C. R. Witte, R. L. Jefferies, and P. J. Weatherhead. 2003. Response of nesting Savannah sparrows to 25 years of habitat change in a snow goose colony. *Ecoscience* 10:33-37.
- Rockwell, R. F., K. F. Abraham, C. R. Witte, P. Matulonis, M. Usai, D. Larsen, F. Cooke, D. Pollak, and R. L. Jefferies. 2009. The Birds of Wapusk National Park. Wapusk National Park of Canada Occasional Paper #1. Winnipeg, Manitoba. Parks Canada.

- Rumpff, L., D. H. Duncan, P. A. Vesk, D. A. Keith, and B. A. Wintle. 2011. State-and-transition modelling for adaptive management of native woodlands. *Biological Conservation* 144:1224–1236.
- Sammler, J. E., D. E. Andersen, and S. K. Skagen. 2008. Population trends of tundra-nesting birds at Cape Churchill, Manitoba, in relation to increasing goose populations. *Condor* 110:325-334.
- Srivastava, D. S., and R. L. Jefferies. 1995. Mosaics of vegetation and soil salinity: A consequence of goose foraging in an arctic salt marsh. *Canadian Journal of Botany*. 73:75-83.